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VOLUME 32 AUGUST 1954 NUMBER 4

THE DEVELOPMENT OF LIFE TABLES FOR THE SPRUCE BUDWORM[1]

BY R. F. MORRIS[2] AND C. A. MILLER[2]

Abstract

A method for preparing life tables is described and two examples are presented, based on field data from the Green River Watershed in northwestern New Brunswick. Column headings for age interval (x), survivorship (l_x), deaths (d_x), and death rate (q_x) are adopted from human life tables. An additional column, d_x factor, should be added to insect life tables so that the different mortality factors can be tabulated. Life tables for the spruce budworm are based on intensive population sampling on permanent plots, complemented by data on fecundity, natural and applied control factors, and dispersion. Techniques for these basic studies will be detailed in subsequent papers. Life tables for consecutive generations of the budworm in different forest types should provide fundamental information on the epidemiology of the species and on the possible reduction of damage through forest management and through direct control measures.

Introduction

This is the first in a series of papers dealing with techniques for studying natural populations of the spruce budworm, *Choristoneura fumiferana* (Clem.). The preparation of life tables is not so much a technique in itself as an objective to be kept in mind while suitable field techniques are being developed. Thus the present paper, describing this objective, will serve as a logical introduction to the series. Although established primarily for the spruce budworm, many of the techniques, and particularly the development of life tables, should be applicable to other species of forest insects.

The Green River Project was established in northwestern New Brunswick in 1944 for the long-term study of spruce budworm epidemiology in relation to forest management (9, 14). Some of the objectives can be satisfied at the conclusion of the budworm outbreak by surveys of damage in relation to forest type and silvicultural treatment. Such surveys are useful but must be complemented by more fundamental work to determine how budworm populations are influenced by forest conditions. Otherwise protective silviculture and management can be formulated only on an empirical basis. For this reason, intensive studies of the insect itself were initiated in different forest types.

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Two approaches to the problem are possible. One is essentially an experimental approach and has been used effectively in recent years in the study of the spruce budworm in the Province of Ontario and in the eastern United States. Separate projects are set up, under groups of investigators, to study specific factors thought to be important in budworm epidemiology. Examples of such projects are those dealing with the flowering condition of balsam fir (4), the role of climate (21), parasites (7), and birds (8). The other approach is essentially observational and involves the study of population and natural mortality factors, with the object of developing life tables for each generation of the budworm in different forest stands. For the Green River studies this latter method was adopted because it had not previously been tried and because it would provide a useful check on conclusions reached through the more experimental studies. The limitation to this approach is the amount of reliable population sampling that can be accomplished at certain stages in the life-history.

The work was initiated before the infestation started in New Brunswick so that its progress could be followed from beginning to end. At the present writing, the outbreak is probably near its peak in the northern part of the Province and may be expected to continue for another five years or more. There will be a rather long period, therefore, before final results of the study become available. Meanwhile field techniques have received much attention and, considering that spruce budworm investigations are of immediate concern in various parts of North America, it seems worth while to present them now. The papers in the present series will be restricted to methodology; beyond examples necessary to illustrate techniques, no results will be presented and no conclusions formulated until the course of the outbreak is completed. It is a common tendency to improve techniques from year to year and, on the basis of added knowledge, the figures in life tables are subject to periodic revision. Although the examples are based on actual field data, the writers reserve the privilege of revising the figures in later publications if additional work suggests that such revision will make them more representative of the true course of events. Further, although the efficacy of a given technique can be tested immediately by biometrical analysis, the final evidence as to the value of the whole approach must await the conclusion of the work when it becomes known whether or not the objectives of the Project have been satisfied.

The Nature of Life Tables

Life tables were first used for human populations, where they underlie actuarial studies, and many life tables may be found in the literature for various countries and smaller political units. Owing to the lack of techniques for measuring natural populations, it is only within the past decade or two that life tables have been attempted for other organisms, or have received treatment in textbooks (1, 10) on ecology.

A definition of the life table is contained in the following (1): "One of the most useful of all numerical aids for the population student is the life

table, a device that records in systematic fashion those facts basic to the age distribution of mortality. In short, a life table 'keeps the books on death'." The column headings conventionally used in life tables are also taken from Allee *et al.* (1), with an arrangement from left to right:

x Age in appropriate units, stated as an interval.

l_x The number surviving at the beginning of the age interval stated in the x column.

d_x The number dying within the age interval stated in the x column.

q_x The number dying in the age interval divided by the number of survivors at the beginning of the interval. *The rate of mortality.*

e_x Life expectation. Mean length of life remaining to each organism alive at the beginning of the age interval.

Leopold (10) was one of the first to appreciate the possibilities of the life table in the field of practical ecology. (Although he uses the term 'life equation', his discussion and examples apply essentially to life tables.) "This collective action of the factors on a given species in a given locality through a typical year may be called the 'life equation'. I strongly recommend that the game manager, even before he has begun the process of measuring the separate factors, attempt to visualize this life equation as a whole, and from end to end, rather than to defer thinking about any factor until he has made enough measurements to assign a local value to it, or to defer thinking about the equation until he has made enough measurements to assign local values to all its factors." The only point of real difference between Leopold's tables and conventional life tables is that he places the emphasis on the mortality attributable to each factor of natural control, rather than on the mere order of dying. Leopold also suggests the method of evaluating the effect of certain control factors by the process of subtraction in the life table. "The essential condition for applying this method of 'analysis by subtraction' is that the annual increment be known, and that the values of some of the subsequent factors of mortality be known. The difference will always be the value of the other factors." As many factors of mortality do not lend themselves to direct measurement, this procedure will be indispensable in the development of life tables in biology, as will be shown in a later paragraph.

Deevey (6) has presented a very useful review of the life table as a tool in the study of natural populations. Using examples from the literature, he illustrates three ways in which life tables may be developed. "(1) Cases where the age at death (d_x) is directly observed for a large and reasonably random sample of the population; (2) cases where the survival (l_x) of a large cohort (born more or less simultaneously) is followed at fairly close intervals throughout its existence; (3) cases where the age structure is obtained from a sample, assumed to be a random sample of the population, and d_x is inferred from the shrinkage between successive age classes. It should be noticed that only the second sort of information is statistically respectable, since insofar as the breeding can safely be assumed to be simultaneous, it is comparable to

that obtained from a *Drosophila* bottle. The first and third types can be used only if one is prepared to assume that the population is stable in time, so that the actual age distribution and the life table age distribution are identical." None of these three methods is directly applicable to the spruce budworm. Although each generation starts as a cohort born more or less simultaneously (most of the eggs are deposited in a period of about two weeks), the life-history and mobility are such that periodic survivorship data cannot be obtained on the same individuals under natural conditions. The method used is therefore a modification of Deevey's second method in that survivorship is measured by periodic sampling of the same population (using branch samples from the same, numbered trees throughout a generation) but not the same individuals. Survivorship figures for the budworm are consequently subject to a sampling error, which can be evaluated biometrically; this was not so for *Drosophila* or *Balanus*.

This review (6) is admittedly confined to the form of the life table (the *order* of dying) and the author points out that such tables are of limited usefulness to the biologist without supporting data on the causes of mortality. It is also difficult to compare life tables published to date for they take their origin at different biological ages. "Is it fair to compare a bird life table, beginning at early adult life, with the Dall sheep life table, which begins at birth, or with the life table of a sessile invertebrate, beginning at attachment or metamorphosis? Evidently not; birth itself is not an age of universal biological equivalence, outside the placental mammals, and for a broader view of comparative mortality the only safe point of reference would be the fertilized ovum."

In the field of forest entomology it is not possible to refer to any life tables that are reasonably complete. (Theoretical tables, prepared to illustrate mathematical theories on population and mortality factors, are outside the scope of the present work.) This results from the fact that adequate field techniques have not yet been developed for most insects. The practical difficulties are great. Most sawflies, for example, pass the larval stage in the tree and the cocoon stage in a different universe, the forest floor; but to develop life tables, techniques must be found to express populations of all stages in terms of a common unit. Considering the present trend towards intensive work on population and mortality factors, however, it is very likely that these problems will be solved and that life tables will be developed for various species in future years. The development of complete life tables and mortality data is the ultimate objective, at least implicitly, of much of the recent ecological work in forest entomology. As early as 1922 Tothill (20) published tables for the fall webworm, *Hyphantria cunea* Drury, which were essentially partial life tables although, as Thompson (19) has already pointed out, they were greatly oversimplified. In 1949 Morris presented tables for both the spruce budworm (11) and the black-headed budworm, *Acleris variana* (Fern.) (12) but they contained gaps because some of the requisite techniques for these species were not fully established at the time.

In concluding this general discussion of life tables, it will be well to indicate how life tables for forest insects are likely to depart from the conventional form. The major divergence, i.e., the emphasis on the causes of mortality rather than the order of dying, has already been referred to. In biological life tables the writers suggest that a new column 'd_x F' (i.e., mortality factor responsible for the corresponding d_x) be inserted immediately to the left of the d_x column. If there are many mortality factors involved, this may have the disadvantage of making the table so long that it cannot readily be visualized as a unit. A practical compromise is to list under d_x factor in the life table the major groups of factors such as parasites, disease, etc.; mortality attributable to each parasite or disease organism can then be detailed in a supplementary table.

In human life tables the age intervals (x column) are generally equal; in life tables for forest insects equal age intervals will be impossible because population measurement is not feasible at certain periods in the life-history when the insect is highly mobile and the population is in process of dispersion or redistribution. The age intervals will generally represent the major stages in the life-history, with such subdivision of the larval stage as is feasible.

The origin of the l_x column in human life tables is conventionally taken as 1000 individuals. In forest entomology, however, it is an important objective to determine how the effect of each mortality factor varies with changes in the population density of the insect from year to year. It is strongly recommended, therefore, that l_x be given as actual population figures in terms of some appropriate sampling unit. This unit must be absolute, of course, in the sense that only the insect population varies in time and not the unit. Similarly, q_x is generally given in human tables as 1000 q_x whereas in forest insect tables it will be more convenient to use 100 q_x, i.e., percentage mortality. The column for e_x is of doubtful value in insect work and is not used in the present paper.

First Example

The first example of a life table (Table I) to be discussed applies to the 1952–53 generation of the spruce budworm on Permanent Plot G4 on the Green River Watershed. This plot is in a stand composed largely of mature balsam fir, *Abies balsamea* (L.) Mill., and all the population sampling, parasite rearings, etc. on which the table is based apply to this host tree. The stand is outside the perimeter of a severe budworm infestation and the population level of budworm was relatively low; loss of new foliage through the feeding of budworm larvae in 1953 was less than 20%.

Knowledge of the life-history of the insect is necessary if the life table is to be understood. This need be described only briefly for it is shown graphically at the top of Fig. 1 and will be further clarified in the explanation of the life table. There is one generation per year which extends over parts of two calendar years; the eggs deposited one summer give rise to the larval feeding stage, the pupal stage, and moth stage of the following summer.

The winter is passed as a second-instar larva in a hibernaculum. In the spring the larvae emerge and feed first on the staminate flowers of the tree (if available) or mine needles and buds; later they enter the swelling buds and still later feed freely on the needles of the expanding shoots. All stages of the insect except the moth in flight are normally found on the tree. Consequently, although population sampling presents many problems, such as the securing of periodic branch samples from heights of up to 60 ft. on standing trees (13), it is simplified by its restriction to one type of universe.

TABLE I

LIFE TABLE FOR THE 1952–53 GENERATION OF THE SPRUCE BUDWORM ON PLOT G4, GREEN RIVER WATERSHED, NEW BRUNSWICK

x	l_x	$d_x F$	d_x	100 q_x
Age interval	No.* alive at beginning of x	Factor responsible for d_x	No.* dying during x	d_x as percentage of l_x
Eggs	174	Parasites	3	2
		Predators	15	9
		Other	1	1
		Total	19	11
Instar I	155	Dispersion, etc.	74.4	48
Hibernacula	80.6	Winter	13.7	17
Instar II	66.9	Dispersion, etc.	42.2	63
Instars III–VI	24.7	Parasites	8.92	36
		Disease	0.54	2
		Birds	3.39	14
		Other — inter.†	10.57	43
		Total	23.42	95
Pupae	1.28	Parasites	0.10	8
		Predators	0.13	10
		Other	0.23	18
		Total	0.46	36
Moths (SR = 50 : 50)	0.82	Sex	0	0
Females ×2	0.82	Size	0	0
		Other	0	0
		Total	0	0
'Normal' females ×2	0.82	—	—	—
GENERATION	—	—	173.18	99.53

Expected eggs	62	Moth migration, etc.	−513	−827
Actual eggs	575			

Index of population trend: Expected 36%
Actual 330%

* *Number per 10 sq. ft. of branch surface.*
† *Other factors minus mutual interference among all factors (see text).*

The reliability of a life table is only as good as that of the basic data on population, fecundity, and mortality factors. Confidence limits have been established biometrically for the data and will be detailed in subsequent papers of the series which deal with these specific subjects. In the interests of uniformity in the present examples we have generally retained three figures in the l_x column and have taken the 100 q_x column to the nearest 1%. All l_x and d_x figures represent individuals per 10 sq. ft. of branch surface, rather than one square foot, to reduce the number of decimal places. The average tree sampled on G4 contained 570 sq. ft.

For Table I, the age intervals (x), with the corresponding l_x, d_x factor, d_x, and 100 q_x, are explained in separate paragraphs for each stage of the insect.

Eggs

l_x is based on direct population sampling after eclosion in August. At this period it is not difficult to determine what proportion has hatched successfully and what proportion (100 q_x) has been killed by parasites or predators, or has failed to hatch through infertility or physiological factors. The choice of actual egg population for the point of origin instead of a theoretical potential will be defended below.

Instar I

l_x is represented simply by the number of eggs that hatched successfully. The tiny larvae wander in search of hibernating sites and generally start to spin hibernacula within a matter of hours after hatching from the eggs. In the wandering process, however, many of them drop on fine threads and are dispersed widely by air currents, which deposit a proportion of them on land, water, or nonhost vegetation. Although predators may take some of the first-instar larvae, it is considered that the wastage through dispersal, either directly or indirectly, represents the main d_x factor. The d_x value of 74.4 is obtained by subtracting 'Hibernacula' from 'Instar I' in the l_x column.

Hibernacula

First-instar larvae in hibernacula molt, in the early fall, to the second instar. It is convenient, however, to treat the hibernacula period as one x unit, regardless of instar. Hibernacula are too small and well concealed to permit direct population sampling, so l_x is determined by a special technique in which the branch samples are first exposed to winter temperatures and then left in special laboratory cages, where the second-instar larvae emerge and collect at a light source. An adequate number of checks in which the number of hibernacula is known must also be used as it is not possible to secure complete emergence by these artificial means. The mortality rate, 100 q_x, is obtained by collecting hibernacula from the plot for dissections and rearings just before spring emergence. This 'winter' mortality is generally low and its causes have not been studied in detail. In preparing the curves (Fig. 1), it was assumed that it occurred at a constant rate throughout the winter.

Instar II

l_x is readily obtained from the line above by deducting winter mortality, and applies to larvae successfully emerging from hibernacula in May, 1953. Again there is a considerable wastage, due largely to dispersion, as these larvae (only about 2 mm. in length) search for suitable feeding sites. Through the action of convection or suitable air currents, a portion of this wastage for either instars I or II may actually represent a redistribution in population from one stand to another; as yet, however, we have no instances where the population on a plot has shown an increase after one of these dispersion periods. The loss (d_x) is estimated by the process of subtraction in the l_x column. In addition to the dispersion loss, d_x includes some mortality which occurs in early feeding sites because the next l_x figure is not obtained until the larvae are at the peak of the third instar. However, special sampling on a few plots during the early mining period indicates that this is low in comparison to the dispersion loss.

Instars III–VI

For several reasons it is not feasible to treat these four instars separately in a life table. Differences among individuals in the rate of development lead to wide overlapping and it is not uncommon to find three instars in the field on the same date (Fig. 1). Also, a given d_x factor commonly affects more than one instar, and to segregate d_x values by instar would present a very difficult problem. The value of l_x for the period is obtained by direct population sampling in early June, when the third instar is the prevalent instar in the field. Total d_x is found by subtracting 'Pupae' from 'Instars III–VI' in the l_x column. The establishment of d_x values for the individual d_x factors operating during this period presents a number of complex problems and is deferred for discussion under a later heading.

Pupae

l_x is established by the direct population sampling of pupal cases in late July, after the moths have emerged. A careful examination of the cases, supported by data from collections and rearings of pupae before emergence, provides the values for d_x. The role of each parasite species is also evaluated, although not detailed separately in the present example. 'Predators' include only invertebrate predators; as sampling of pupae is delayed until the emergence period is over, the predation on sound pupae by birds and mammals, which consume case and all, is included above under 'Instars III–VI'. This is explained more fully below. 'Other factors' include physiological factors and disease, and can be subdivided when the effects of the different diseases are more fully understood.

Moths

l_x is represented by the number of pupal cases showing successful adult emergence and sex can be determined from the same cases. In the present example the normal sex ratio of 50 : 50 applies. If this should be distorted

in favor of males it would represent, *in effect*, a source of mortality associated with the present generation; so sex is listed as a d_x factor.

Females

This is simply the percentage of females applied to l_x for moths. The result must be doubled, of course, to maintain balance in the life table. If the body size of the average female is reduced, through food shortage in the larval period or unfavorable developmental conditions, this also represents, *in effect*, a d_x factor arising in the present budworm generation. The fecundity of the females is reduced in proportion to body size and the relationship between fecundity and moth or pupal measurements will be detailed in a later paper. On Plot G4 there was no food shortage in 1953 and female size was normal. A line has been inserted under d_x factors to take care of factors other than female size which might reduce fecundity; however, there is no evidence that such factors are operative in the Green River population to date. The treatment of sex ratio and fecundity will become clearer in our second example, where both are abnormal.

Normal Females

l_x represents the number of 'normal females', i.e., the number of females capable of laying a normal complement of eggs. It is a hypothetical figure but in the present example corresponds to the actual number of females. We can now compute d_x for the whole generation, either by subtraction in the l_x column ('Eggs' − 'Normal females × 2') or by accumulation in the d_x column. In the present example, mortality for the whole generation is 99.53%. As the normal sex ratio of the budworm is 50 : 50 and the mean oviposition is 150 eggs per female, the mortality rate for a constant population level is $100(148/150) = 98.67\%$.

As an alternative method, the life table for the generation could be terminated immediately after l_x for moths. The following generation would then start with potential eggs rather than actual eggs, and the d_x factors for potential eggs would include abnormal sex ratio and reduced fecundity. It seems illogical, however, to defer to the new generation those d_x factors which clearly have their source in food shortage or other unfavorable conditions during the current generation.

It is the object on permanent plots to prepare life tables for each succeeding generation of the budworm through the rise and fall of the epidemic. The table for one generation should be arithmetically continuous, in fact, with those for the preceding and following generations. It is necessary, therefore, to insert a few lines (Table I) at the bottom of the life table for each generation.

Expected Eggs

l_x is the number of 'normal' females (in this case 0.41) multiplied by 150. The same result would be obtained, of course, by using actual females and multiplying by the appropriate oviposition figure depending on body size. The actual egg population may be either greater or less than the expected

through such factors as moth migration into the area, moth migration out of the area, mating failure, mortality of females before oviposition is completed. The effects of these factors are very difficult to separate quantitatively. In the present example there is clearly a case of moth invasion into the stand, presumably from severely infested stands nearby, and the invaders have added 513 eggs per 10 sq. ft. to the 62 eggs expected from the local moths. That such invasion must have occurred can be demonstrated statistically by means of an analysis of variance of the population data.

Eggs

l_x is determined by direct population sampling in August and forms the life table origin for the next generation of the budworm on Plot G4.

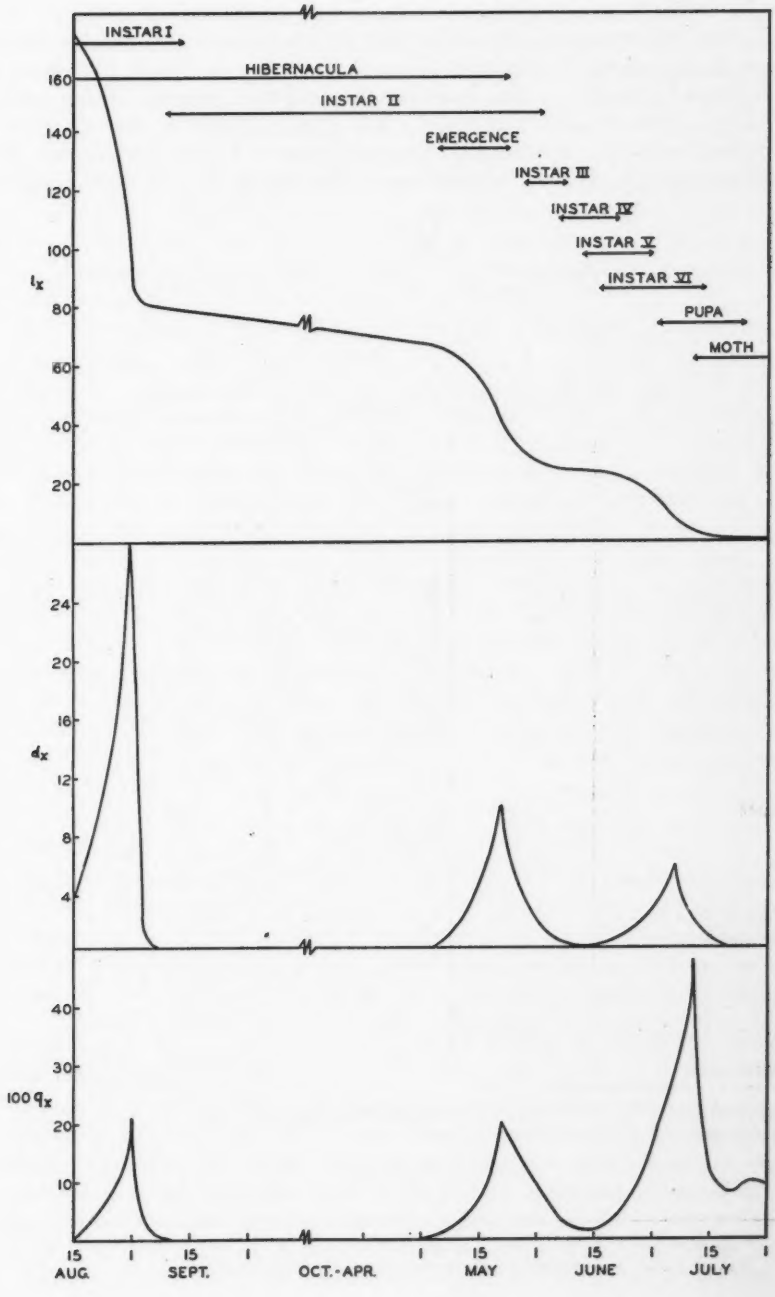
Index of Population Trend

This term is borrowed from Balch and Bird (2) and is simply l_x for the new generation expressed as a percentage of l_x for the old generation, at the same point in the life cycle. In the present example this has a value of $100(62/174) = 36\%$, based on the number of expected eggs. Thus, d_x factors during the current generation should have resulted in a considerable decline in the annual population trend. As a result of moth invasion, however, the actual index of population trend is 330%.

The reader will have noticed in studying Table I that no terms or values have been assigned for such parameters as 'biotic potential' or 'reproductive potential', as defined by Chapman (5). The value of 150 that has been used for fecundity represents the mean number of eggs deposited by females of normal size when protected from predators by cages of wire mesh. Thus no d_x factor occurs in the table to represent the difference between 150 and the hypothetical maximum for the species. Even if there were some practical way to establish this parameter, the associated rate of mortality between the potential and the actual would be constant in all life tables prepared to date for Green River and would add nothing to plot comparisons.

The survivorship, death, and death-rate curves (Fig. 1) are based on the life table (Table I) along with supplementary information on the rate of development and the shape of the population trend over certain periods. The survivorship (l_x) curve was drawn first and a new life table was prepared (omitting 'd_x F') for short constant intervals of one or two days. From this new table the d_x and 100 q_x curves were readily established. Thus all three curves are arithmetically compatible. Unlike curves presented to date for other organisms, the survivorship curve for the spruce budworm has several points of inflection and cannot be classified simply in any of Pearl's three groups (16). At different points in the curve the slope corresponds to that for the 'rectangular', the 'intermediate', and the 'diagonal' types.

FIG 1. Survivorship (l_x), mortality (d_x), and percentage mortality (100 q_x) curves for the 1952–53 generation of the spruce budworm on Plot G4, Green River Watershed, New Brunswick. The curves for l_x and d_x represent number of insects per 10 sq. ft. of branch surface.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1

Second Example

The second example (Table II) follows the form of the first and illustrates a few d_x factors which had zero values in Table I. It applies to the same generation (1952–53) of the budworm in a similar mature balsam stand (Plot G9), about 12 miles east of G4. This stand, however, is well within the severe outbreak area and the 1952 egg population of 2176 was well above the level necessary to ensure complete loss of new foliage through larval feeding

TABLE II

LIFE TABLE FOR THE 1952–53 GENERATION OF THE SPRUCE BUDWORM ON PLOT G9, GREEN RIVER WATERSHED, NEW BRUNSWICK

x	l_x	$d_x F$	d_x	100 q_x
Age interval	No.* alive at beginning of x	Factor responsible for d_x	No.* dying during x	d_x as percentage of l_x
Eggs	2176	Parasites	1	< 1
		Predators	174	8
		Other	21	1
		Total	196	9
Instar I	1980	Dispersion, etc.	1148	58
Hibernacula	832	Winter	141	17
Instar II	691	Dispersion, etc.	484	70
Instars III–VI	207	Parasites	2.9	1
		Disease	0.3	< 1
		Birds	1.7	1
		Starvation	165.3	80
		DDT	8.3	4
		Other – inter.†	26.7	13
		Total	205.2	99
Pupae	1.80	Parasites	0.13	7
		Predators	0.11	6
		Other	0.27	15
		Total	0.51	28
Moths (SR = 54 : 46)	1.29	Sex	0.10	8
Females ×2	1.19	Size	0.57	48
		Other	0.00	0
		Total	0.57	48
'Normal' females ×2	0.62	—	—	—
GENERATION	—	—	2175.38	99.97
Expected eggs	47	Moth migration, etc. −199		−423
Actual eggs	246			

Index of population trend: Expected 2%
Actual 11%

* *Number per 10 sq. ft. of branch surface.*
† *Other factors minus mutual interference among all factors (see text).*

in 1953. The larval population, however, was affected by two unusual factors in 1953. A series of frosts in late May and early June, when the buds were swelling, destroyed 59% of the buds on balsam fir. While the frost did not kill budworm larvae directly, many larvae died of starvation because early-instar larvae cannot develop on old foliage. Then, on June 28, the area was treated with an insecticide (DDT) applied from aircraft, as a part of the large-scale spraying operation conducted in New Brunswick in 1953. Life tables are available for a second plot in the outbreak area, which was affected by frost but not by spray, and for a third, which was affected by neither frost nor spray. By comparing the three life tables it is possible to evaluate the effects of the frost and the spray separately.

The d_x values for the first part of the life table (Table II) are similar to those for Plot G4. The period 'Instars III–VI' is an exception and will be discussed for both plots under a later heading. On G9 the sex ratio was slightly distorted in favor of males. This has the effect of a d_x factor reducing the population of females by 8%. Also, the size of the females was considerably reduced below normal. Frost damage and early feeding exhausted the new foliage and forced late-instar larvae that survived the DDT to feed on old foliage. Small pupae resulted and the emerging females could lay only 78 eggs instead of the normal 150. This has the effect of a d_x factor reducing the moth population by 48%. Total mortality for the generation is 99.97% and the expected index of population trend only 2%. However, as happened on certain other plots in 1953, moth dispersion into the area gave an actual egg population significantly higher than the expected. This has the opposite effect to d_x and must be preceded by a minus sign when listed under the d_x column (Table II). This invasion, while ensuring at least a moderate degree of defoliation for the following year, increases the index of population trend to only 11%.

Instars III–VI

These four instars, during which practically all the feeding is done, represent a brief but dynamic and important interval in the life-cycle. To find an exact value for the d_x attributable to each mortality factor is very difficult because dead larvae, unlike eggs and pupae, leave behind no shells or cases from which their fate may be determined. Total mortality for 'Instars III–VI' is readily obtainable but mortality from individual factors can be represented only by potential values which are subject to the influence of mutual interference.

The method of dealing with these instars is best demonstrated by subdividing the larval interval. Although subdivision by instars is not feasible, the writers have found it convenient to divide the whole interval into four periods corresponding, in general, to periods when certain important parasites are causing mortality. The l_x for each period is obtained by direct population sampling but this sampling is generally less intensive than that used in establishing l_x for the major intervals of the life table. Also, during the late

instars, population work becomes more difficult because free-feeding larvae readily drop from the foliage when the branch is disturbed.

The dates for these periods vary somewhat from year to year, depending on larval development, but in general they are as follows:

Period 1.—First week in June to about June 17, i.e., from peak abundance of the third instar to peak abundance of the fourth. In this period no mortality is caused by parasites and the larvae are probably too small and well concealed to suffer greatly from predators; in fact, many of the migratory birds are just arriving during this period.

Period 2.—June 17 to late June or early July, i.e., from peak of fourth instar nearly to peak of the sixth. *Apanteles fumiferanae* (Vier.) destroys the host larva and emerges during this period.

Period 3.—Late June or early July to about July 10, i.e., from peak of sixth instar to late sixth instar and early pupae. *Glypta fumiferanae* (Vier.) causes mortality in this period.

Period 4.—July 10 to late July, when adults have emerged from pupae. *Meteorus trachynotus* Vier. and a number of Dipterous parasites emerge from the host larvae in this period.

A life table for 'Instars III–VI' on Plot G4, expanded to show the four periods, may be found in Table III. For each parasite, 100 q_x is obtained by the dissection or rearing of collected budworm larvae and represents the percentage parasitism at the beginning of the appropriate period. That is, 100 q_x is the percentage parasitism of the host population as measured just before the parasite completes development and kills the host larva. The corresponding d_x represents the number of larvae that would be killed by the parasite *if nothing interfered.* However, during the period when the parasite is emerging, which may be two weeks or longer, both parasitized and unparasitized host larvae are subject to considerable mortality from other factors. Thus, d_x represents only a potential value; the problem of finding the actual value has not been solved.

The same method is applied to larval diseases. Larvae are collected at random from the plot in individual gelatin capsules and blood smears are examined by special microscopic techniques. This provides the percentage infection by disease and again d_x represents potential rather than actual mortality. A capsule virus showed a percentage infection of over 50% in 1953 but it was clearly not fatal to the larvae and has been excluded from the life table. A microsporidial disease and a polyhedral virus were found to a smaller extent and, for purposes of illustration, it is assumed that they caused mortality to mature larvae (Table III). Some revision of life tables will be necessary when the effects of disease on both larvae and pupae are known.

The d_x estimate for insectivorous birds also represents a potential rather than an actual figure. As will be detailed in a later paper, it is obtained from a consideration of (1) the food capacity of birds with reference to the budworm,

TABLE III

SUPPLEMENT TO TABLE I FOR PLOT G4, SHOWING DIVISION OF INSTARS III–VI INTO FOUR PERIODS (SEE TEXT)

x	l_x	$d_x F$	d_x	100 q_x
Instars III–VI:	24.7	—	—	—
Period 1	24.7	Miscellaneous	1.4	6
Period 2	23.3	*A. fumiferanae**	5.1	22
		Birds	1.1	4
		Other – inter.	2.7	12
		Total	8.9	38
Period 3	14.4	*G. fumiferanae*†	1.6	11
		Birds	1.1	8
		Other – inter.	5.7	39
		Total	8.4	58
Period 4	6.0	*M. trachynotus*‡	1.38	23
		G. interrupta§	0.48	8
		Other Diptera	0.36	6
		Disease	0.54	9
		Birds	1.19	20
		Other – inter.	0.77	13
		Total	4.72	79
Pupae	1.28	—	—	—

* *Apanteles fumiferanae* (*Vier.*), *predominantly, but includes other species of Apanteles.*
† *Glypta fumiferanae* (*Vier.*).
‡ *Meteorus trachynotus Vier.*
§ *Gymnophthalma interrupta* (*Curr.*).

(2) an annual breeding census to obtain population per acre on the plot, and (3) conversion of budworm population per unit of foliage surface to population per acre. For Plot G4 in 1953, the potential consumption of budworm larvae and pupae by birds was 3.39 per 10 sq. ft. (Table I). It is assumed that this may be about equally divided among the last three periods (Table III).

All the d_x values for specific factors are therefore only potential, so to balance the life table another line—'Other factors minus mutual interference'—must be added. Other factors include unfavorable climatic conditions, invertebrate predators, arboreal mammals, physiological factors, dispersion loss, and misadventures. Techniques for assigning d_x estimates to such factors have not been developed but in any case their composite d_x will be a positive number. Interference, on the other hand, gives rise to a negative number representing the amount by which the accumulated d_x for all specific factors is reduced below the potential through mutual interference. If certain assumptions are risked, an attempt can be made to solve the interference problem. To find actual control by parasites, for instance, it may be assumed (1) that all other factors interfere and (2) that parasitized host larvae are

neither more nor less vulnerable to these other factors than are healthy larvae. Until such assumptions have received further study, however, their application in the revision of life tables is open to question.

For any factor the sum of d_x for all periods (Table III) is equal to its d_x value for the whole interval (Table I). The values for 100 q_x do not correspond, however, because in Table I they must all be based on l_x for the third instar. This reduces the percentage figures for factors operating in the late larval period. For example, *M. trachynotus* has a 100 q_x of 23% (Table III); but when the d_x of 1.38 is referred to an l_x value of 24.7 (Table I), this reduces to 5.6%. In a restricted sense (as we are now dealing with only the larval stage) the percentage mortalities in Table I would be defined by Thompson (18) as 'real mortality' and those in Table III as 'apparent mortality'. Some authors (7) have used the formula for 'real mortality' to find an 'aggregate percentage mortality' for one group of factors acting in sequence, excluding simultaneous reductions in population through other groups. These points are mentioned not to introduce the question of the relative effectiveness of mortality factors, but only to clarify the relationship between Tables I and III.

Mortality from parasites, disease, and birds for each larval period on Plot G9 (Table IV) is based on the methods described for Plot G4. In common with other plots in the severe infestation area, G9 shows a lower rate of parasitism than G4. The d_x expected from insectivorous birds is also lower. Although bird populations per acre were somewhat higher in the infestation area, this was more than offset by the greater stand density of G9, resulting in a smaller bird population in relation to foliage area.

The d_x value for early starvation was obtained by comparing the larval population trend of G9 with that of a nearby plot which escaped the frost damage. As the two plots were reasonably similar as to initial larval population, the assumption was made that the trends would have been similar in the absence of any frost damage. In Period 1, there was a total population reduction of 79% on G9 (Table IV), in contrast to a 7% reduction on the plot escaping frost damage. The difference of 72% may be attributed to unusual starvation. Again, because of interference, the corresponding d_x of 149 for starvation cannot be considered a true value. We can only say that when starvation was added to the complex of other factors it increased d_x by 149; conceivably it may have so interfered with the other factors that the total d_x of 164 resulted directly from starvation.

The d_x resulting from DDT in Period 3 was obtained in the same way, by comparing G9 to a check plot where the population was subject to a similar degree of starvation but not to insecticide. The same limitations apply, the addition of DDT to the other factors increased total d_x by 8.3 but the d_x resulting directly from DDT cannot be determined until the nature of its interference with parasites and other factors is understood.

The 44% mortality listed for DDT (Table IV) is much lower than the control figures usually attributed to aerial spraying. This results from the

TABLE IV

SUPPLEMENT TO TABLE II FOR PLOT G9, SHOWING DIVISION OF INSTARS III–VI INTO FOUR PERIODS (SEE TEXT)

x	l_x	$d_x F$	d_x	100 q_x
Instars III–VI:	207	—	—	—
Period 1	207	Starvation	149	72
		Other – inter.	15	7
		Total	164	79
Period 2	43	*A. fumiferanae*	1.3	3
		Birds	0.5	1
		Starvation	16.3	38
		Other – inter.	5.9	14
		Total	24.0	56
Period 3	19	*G. fumiferanae*	1.5	8
		Birds	0.6	3
		DDT	8.3	44
		Other – inter.	5.7	30
		Total	16.1	85
Period 4	2.90	*M. trachynotus*	0.03	1
		Diptera	0.11	4
		Disease	0.26	9
		Birds	0.56	19
		Other – inter.	0.14	5
		Total	1.10	38
Pupae	1.80	—	—	—

fact that the effectiveness of applied control measures, whether determined by Abbott's formula* or by direct comparison of residual populations, is conventionally based on *survival* population rather than the population at the time of treatment. In the present example the survival on G9 was 2.90 (Table IV), whereas in the absence of spraying it would have been 2.90 + 8.3 = 11.2. Control based on survival population is 100 × 8.3/11.2 = 74%, as compared to the 44% of Table IV. If this is carried a step further and based on survival at the end of the pupal stage, the control figure can be increased to over 80%. Natural mortality factors like parasites and disease, on the other hand, are commonly assessed according to the percentage of larvae affected, as in the life tables. This basic difference in the derivation of mortality figures extends through the entomological literature and is possibly the reason why one author (3) has proposed the use of 'mortality/survival ratios' for all types of mortality factors. However, when mortality is based on survival population, a basic weakness is that the percentage figures for a given factor do not lend themselves to direct comparisons from year to year

* *$100(x - y)/x$ = % control, where x = % survival in check population and y = % survival in treated population.*

or from place to place, for they vary with the degree of mortality resulting from other factors. Let us say, for example, that factor '*A*' always causes an additional 25% mortality of larvae when added to other mortality factors '*F*'. In one instance *F* reduces an initial population of 100 larvae to a population of 90, as determined in a check area, so that the addition of *A* reduces a similar population to 65. The effect of *A*, based on survival population, is $100(90 - 65)/90 = 27\frac{7}{9}\%$. If, however, *F* reduced the check population to 30, the effect of *A* on survival is increased to $83\frac{1}{3}\%$, although no intrinsic change has taken place in the direct effect of *A* on the insects. As illustrated above, variations also arise depending upon how soon after the treatment the effect on survival is calculated.

Regardless of how the investigator may wish to compare the relative effectiveness of different control factors, life tables should provide the basic information. Once they are completed, 'apparent mortality', 'real mortality', 'mortality/survival ratios', or any similar transformations can readily be made.

The Application of Life Tables

To the practical biologist life tables will be valuable only in so far as they further the understanding of the fundamental epidemiology of the species and aid in the development of control measures. By control we refer particularly to the prevention of important economic damage, whether it be achieved by the manipulation of the biotic environment or by more direct methods. A life table for one generation of the insect in one environment is unlikely to be very helpful in this respect, beyond indicating 'weak points' in the life-cycle where natural mortality is very high. For the spruce budworm such points occur in the dispersion periods of the first and second instars and in the late feeding instars (Fig. 1). More valuable information can be shown, however, by continuous life tables for many generations and for different environments. Nicholson (15) writes, "If an attempt is made to assess the relative importance of the various factors known to influence a population, no reliance whatever must be placed upon the proportion of animals destroyed by each. Instead, we must find which of the factors are influenced, and how readily they are influenced, by changes in the density of animals". Life tables should reveal the influence of changes, not only in density but in climatic conditions and environment.

The factors believed to be of importance in the epidemiology of the spruce budworm and in the resulting degree of damage are reviewed by Prebble and Morris (17). It is hoped that the life tables being accumulated will provide new and useful information on the influence of such factors, with respect to both the degree of influence and the stage of the insect affected. The role of staminate flower production by balsam fir, for instance, lends itself to analysis by the comparison of life tables for flowering and nonflowering stands, and for flowering and nonflowering years in the same stand. Similarly, the comparison of life tables over a period of years should show the influence of stand density and composition, both in large forest areas and in small blocks isolated by

cutting operations. Continuous meteorological records are maintained for use in conjunction with the life tables. Other factors, already discussed briefly in connection with the examples presented above, include parasites, predators, exhaustion of food supply, chemical control, and the dispersion of moths and small larvae.

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A SEQUENTIAL SAMPLING TECHNIQUE FOR SPRUCE BUDWORM EGG SURVEYS[1]

By R. F. Morris[2]

Abstract

The object in extensive spruce budworm egg surveys is to classify the infestation as light, moderate, or severe, at a large number of sampling points. The sequential plan, having no fixed sample size, was tested in 1953. It proved very useful, particularly in eliminating superfluous sampling at points where the infestation was definitely light or definitely severe. Curves showing operating characteristics and average sample numbers in relation to population mean permitted an appraisal of the plan in advance of the field test. Field parties were provided with simple tabulations prepared from the acceptance and rejection lines. With an expenditure of 1300 man-days, more than 1000 points were classified in northern New Brunswick.

Introduction

For forest insect surveys it is desirable to have population techniques which permit the rapid classification of infestations at many sampling points. Broad classifications, such as 'light', 'moderate', and 'severe' are generally acceptable, and with an adequate number of well distributed sampling points, infestation maps can be prepared for large areas. For the spruce budworm, *Choristoneura fumiferana* (Clem.), egg surveys in August and September are particularly important for they provide a means of forecasting the damage to be expected from larval feeding in the following year. The aerial spraying program in New Brunswick requires extensive egg surveys because the areas must be selected for treatment and the logistic problems solved before anything is known of spring larval populations. Egg sampling is also necessary after spraying to determine the degree of reinfestation through moth dispersion.

The sequential plan, having no fixed sample size, is well suited to such surveys and permits the classification of infestation level within predetermined limits of accuracy.

This paper is the second in a series (5) concerned with the development of techniques for studying natural populations of the spruce budworm. The sequential analysis to be described was applied in 1953 to meet immediate needs, and was really a by-product from more fundamental population research which has been in progress for several years. Logically, a treatment of the more fundamental studies should precede the present paper in the series. However, the sequential tabulations (Table III) have already been applied rather extensively by field parties in New Brunswick and Quebec, and it seems desirable to describe their mathematical basis without further delay.

Sampling Methods

The tree is the major sample unit and for present purposes we are directly concerned with inter-tree rather than intra-tree variation in population. It

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will be shown in a later paper that the former constitutes the major source of variance when the object is to establish mean population for a given stand or sampling point. For survey purposes it is expedient to restrict the universe to one host species (generally *Abies balsamea* (L.) Mill.) and to the dominant and codominant crown classes. With these restrictions, two methods are available to field parties, depending upon the size of the trees at each sampling point:

Method I.—For very tall trees where the approximate middle of the living crown cannot be reached with pole pruners, the trees are felled and the sample branches selected in the following proportions: one branch from the apical quarter of the crown, one from the second quarter, one-half of a branch from the third quarter, and one-half from the basal quarter. These proportions ensure that the *intensity* of sampling is approximately equal for the different quarters. The sample branches can be pooled to give a mean for the tree without the necessity of weighting, regardless of the vertical distribution of eggs within the crown.

Method II.—Where the approximate middle of the living crown can be reached with pole pruners, one sample branch is selected from the mid-crown of each tree.

These two methods are designed to give maximum return for expended effort. The time required to fell large trees or to use elaborate climbing apparatus makes it worth while to examine a larger quantity of foliage from each tree, since slightly less than one-half as many trees are required by Method I as by Method II. On the other hand, Method II provides a mean with less expenditure of time when the sample branch is easily obtained with pole pruners.

The entire branch except the nonfoliated basal stem is collected. Where only one-half of the branch is to be used, the branch is divided *longitudinally* by discarding all secondaries from one side of the primary stem. The length of the foliated part is then measured as well as the width at mid-length. These two measurements, taken to the nearest 0.1 ft., are multiplied to give an expression of foliage surface. The result is not, of course, a true measure of the foliage area, but only a simple means for reducing the variation attributable to branch size. Population is commonly expressed as the number of egg masses per 100 sq. ft. of foliage surface, as this avoids decimal values.

There are certain errors inherent in egg sampling regardless of the sampling scheme to be used. A proportion of the masses is invariably missed by the first worker who examines the foliage, and it is recommended that at least a partial check be conducted by a different worker (3). Sampling can be extended considerably beyond the period of eclosion but some experience is necessary to separate the newly-emerged masses from the old ones of the previous year. About 25% of the emerged masses of one year are retained on the needles until the egg sampling period of the following year. On the needles of the current year, all masses must be new; on older needles they may be new or old. New masses are semitransparent and fresh looking.

They are generally erect but sometimes collapsed and flat against the needle. Old masses generally appear opaque or dirty and are usually collapsed. Borderline cases are encountered but after experience has been gained, this source of error can be minimized. Egg masses parasitized by *Trichogramma minutum* (Riley) are black and are not usually retained on the needles for a full year.

Infestation Classes

It is desirable that the infestation limits set for egg population should conform approximately to the degree of defoliation expected from the larval population in the following season. This has been achieved through a consideration of (1) accumulated records of average mortality between the egg stage and the feeding larval stage and (2) accumulated records on permanent plots of egg population in one year and defoliation in the following year. The following limits are in general agreement with conventional infestation classes used by the Forest Insect Survey (8):

Infestation	No. of egg masses per 100 sq. ft.
Light	25 or less
Moderate	Between 50 and 100
Severe	More than 200

Since many variables are involved, these classes should not be accepted too literally. An unusually high or low mortality between egg and larval stages can alter the relationship between egg population and defoliation. Also, after trees have been weakened by several consecutive years of severe defoliation, foliage production may be so reduced that a relatively moderate egg population can result in severe defoliation. Foliage production by balsam fir is also greatly reduced in heavy seed years (2). A knowledge of local conditions and of infestation history should govern the application of the above limits, or the establishment of alternative limits. A portion of the collected masses should be examined each year to determine whether important deviations occur from the indicated mean of about 18 eggs per mass.

The Sequential Plan

The first step in the application of the sequential plan is to establish the nature of the frequency distribution, because this determines the formulae to be used in the subsequent steps. Examples of sequential analysis applied to biological sampling problems are provided by Oakland for the binomial distribution (7) and the negative binomial (6), Stark for the normal (9), and Morris (using methods provided by Oakland) for the Poisson (4). Budworm populations measured by the foliage surface method conform very well to the negative binomial, $(q-p)^{-k}$. This was determined by establishing the relationship between mean and variance (s^2) for many sets of sampling data covering a wide range of population means. (These data will be presented in

a forthcoming paper in the present series.) For the negative binomial, the variance of the distribution is given by $m + (m^2/k)$, where m is the mean and k a constant.

The next step is to find a value for k, and Anscombe (1) has presented several methods of computing k for the negative binomial. In the present example, the background data include many sets of counts at different levels of m, so a pooled estimate of k is required. By pooling the variance from all sets of counts and equating it to the theoretical variance, $\Sigma s^2 = \Sigma m + \Sigma m^2/k$, an estimate of k can be obtained. This estimate should then be tested and revised as necessary by one of the methods of Anscombe (1) most appropriate to the data; in the present case Anscombe's formula No. 8 was applied. For Sampling Method I, $k = 5.232$ and for Method II, $k = 2.019$. These estimates are based on all data available up to the end of the 1952 field season; as additional data are gathered further revision will be advisable. Anscombe (1) refers to theoretical evidence suggesting that k depends on the intrinsic power of the species to reproduce itself, while m depends on external factors. For a given sampling method, therefore, k should remain relatively constant within reasonable limits of m. The present data show some tendency for k to increase with m; this was also observed by Anscombe (1).

Referring back to the infestation classes, we may now set up alternative hypotheses (H_0 and H_1) as follows:

To distinguish between light and moderate infestations:

H_0 — that the number of egg masses is 25 or less per 100 sq. ft. (light).

H_1 — that the number of egg masses is 50 or more per 100 sq. ft. (moderate).

To distinguish between moderate and severe infestations:

H_0 — that the number of egg masses is 100 or less per 100 sq. ft. (moderate).

H_1 — that the number of egg masses is 200 or more per 100 sq. ft. (severe).

The values of the constants under each of these hypotheses are now readily established as shown in Table I, using the properties of the negative binomial.

TABLE I

VALUES OF THE DISTRIBUTION CONSTANTS UNDER THE ALTERNATIVE HYPOTHESES, H_0 AND H_1

Constant	Infestation		Infestation	
	Light	Moderate	Moderate	Severe
	H_0	H_1	H_0	H_1
Sampling Method I, $k = 5.232$				
Mean $= kp$	$kp_0 = 25$	$kp_1 = 50$	$kp_0 = 100$	$kp_1 = 200$
$p = kp/k$	$p_0 = 4.7783$	$p_1 = 9.5566$	$p_0 = 19.1131$	$p_1 = 38.2263$
$q = 1 + p$	$q_0 = 5.7783$	$q_1 = 10.5566$	$q_0 = 20.1131$	$q_1 = 39.2263$
Variance $= kpq$	$kp_0 q_0 = 144.458$	$kp_1 q_1 = 527.830$	$kp_0 q_0 = 2011.31$	$kp_1 q_1 = 7845.26$
Sampling Method II, $k = 2.019$				
Mean $= kp$	$kp_0 = .25$	$kp_1 = 50$	$kp_0 = 100$	$kp_1 = 200$
$p = kp/k$	$p_0 = 12.3824$	$p_1 = 24.7647$	$p_0 = 49.5295$	$p_1 = 99.0589$
$q = 1 + p$	$q_0 = 13.3824$	$q_1 = 25.7647$	$q_0 = 50.5295$	$q_1 = 100.0589$
Variance $= kpq$	$kp_0 q_0 = 334.560$	$kp_1 q_1 = 1288.235$	$kp_0 q_0 = 5052.95$	$kp_1 q_1 = 20011.78$

Each pair of hypotheses (H_0 and H_1) is attended by two types of error:

α = the probability of accepting H_1 when H_0 is, in fact, the true situation.

β = the probability of accepting H_0 when H_1 is, in fact, the true situation.

For budworm egg-mass surveys, both α and β have been set at 0.10. Thus, there are 10 chances in 100 that a given sampling point will be classified incorrectly as between light and moderate, or between moderate and severe. Acceptance of this probability of error seems justified in the present situation because (1) it reduces the number of trees that must be sampled at each point, thereby permitting better coverage of large areas, and (2) the survey data are commonly plotted on a map where scattered aberrant points are discounted in the plotting of infestation boundaries.

Calculation of Acceptance and Rejection Lines

All the remaining calculations follow the procedure used by Oakland for whitefish sampling (6), with the exception that we are concerned with two sampling methods and three infestation classes, whereas he was concerned with one sampling method and two classes. This does not alter the procedure and the remaining steps can be shown adequately by dealing only with Sampling Method I, light versus moderate infestation.

The formulae for the acceptance and rejection lines are:

$$d = sn + h_0$$

and

$$d = sn + h_1$$

where the slope of the lines

$$s = k\frac{\log (q_1/q_0)}{\log (p_1 q_0/p_0 q_1)} = 34.846$$

and the intercepts

$$h_0 = \frac{\log B}{\log (p_1 q_0/p_0 q_1)} = -26.613 \text{ where } B = \frac{\beta}{1-\alpha},$$

$$h_1 = \frac{\log A}{\log (p_1 q_0/p_0 q_1)} = +24.284 \text{ where } A = \frac{1-\beta}{\alpha}.$$

We accept H_0, if $d \leq 34.846 - 26.613$.

We accept H_1, if $d \geq 34.846 + 24.284$, where d is the cumulative number of egg masses per 100 sq. ft. and n is the number of trees sampled.

These acceptance and rejection lines are plotted (Fig. 1), as well as the corresponding lines for the moderate versus severe infestation classes. This graph may be used in the field to determine how many trees should be sampled at each point in order to define the infestation class within the accepted limits of α and β. It is helpful to visualize each pair of lines as enclosing a band from which the plotted points must 'escape' before the infestation class is satisfactorily defined. For example, the first tree sampled at a given point shows 200 egg masses per 100 sq. ft. When this is plotted over Tree 1 (Fig. 1), it is seen that we have already escaped the light–moderate band but are still within the moderate–heavy band. The second tree shows 150 masses, so 200 + 150 = 350 masses is plotted over Tree 2, leaving us still in the moderate–heavy band. A third tree is therefore sampled and shows 350

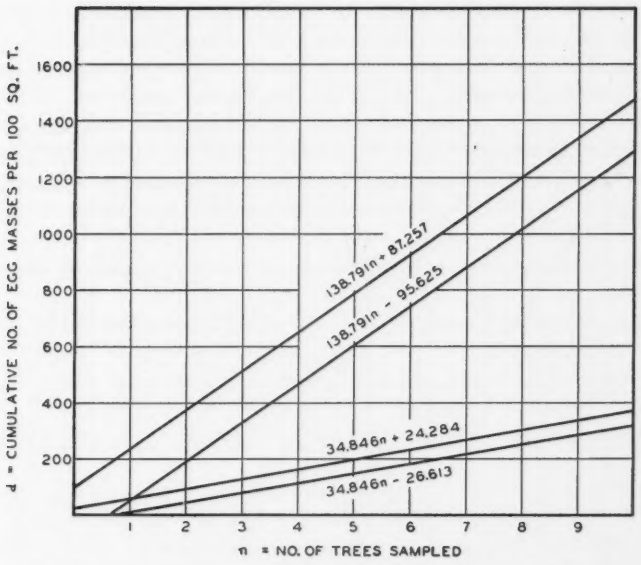

FIG. 1. The acceptance and rejection lines for Sampling Method I.

masses. The cumulated 700 masses plotted over Tree 3 puts us outside the band into the heavy infestation class, and sampling is discontinued. If the plotted points had escaped into the area between the two bands, the infestation would be classed as moderate, and if below the lower band, the infestation would be classed as light. A similar graph (Fig. 2) is available for Sampling Method II.

The Operating Characteristic Curves

The operating characteristic curves and the average sample number curves are not essential in the application of the sequential plan, and their calculation is therefore optional. However, they are useful aids in understanding how the plan operates and in predicting the probable number of trees which must be sampled at different population levels. The calculations follow Oakland (6), with the exception that the writer has found it helpful to use the mean, kp, as the abscissa rather than p.

The operating characteristic curves (Fig. 3) show the probability, $L(p)$, of accepting H_0 for any possible level of the population mean. When the mean, kp, is 25, the probability of accepting H_0 (light infestation) is 0.9 (Fig. 3, curve on left); hence the probability of accepting H_1 (moderate infestation) is 0.1. When $kp = 50$, $L(p) = 0.1$ for H_0 and consequently 0.9 for H_1. At these two levels of kp, the probabilities correspond, of course, to those previously set for α and β. As kp decreases below 25, $L(p)$ for H_0 becomes very high and as it increases above 50, $L(p)$ for H_0 becomes very low. At one

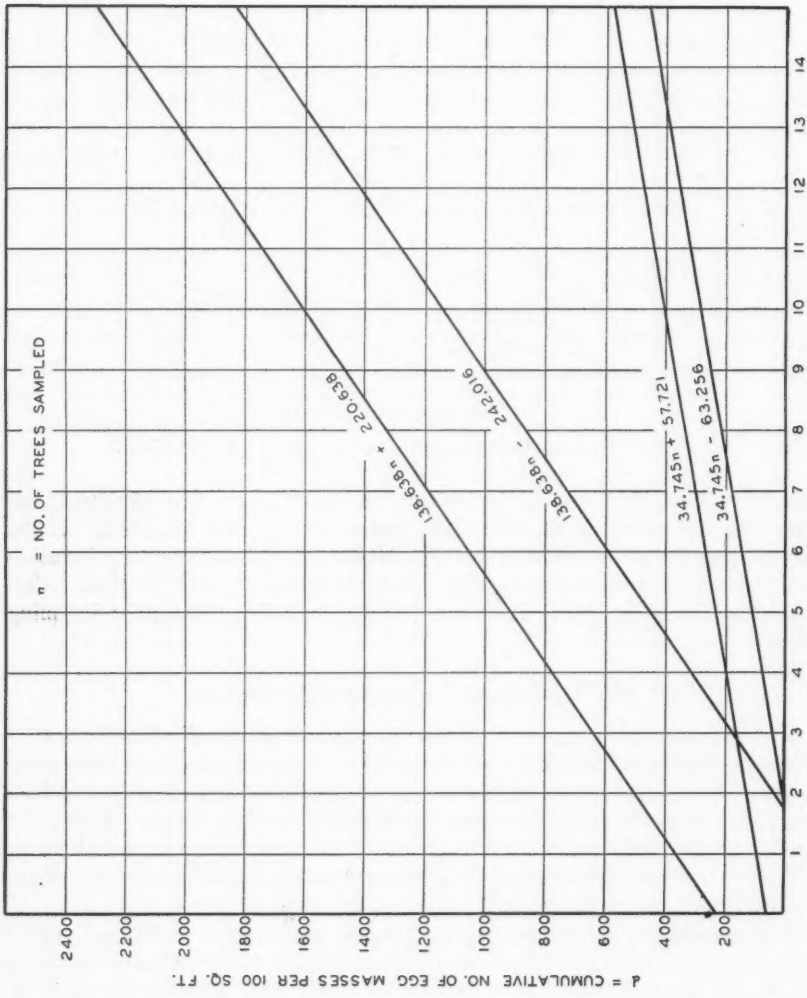

FIG. 2. The acceptance and rejection lines for Sampling Method II.

intermediate population level ($kp = 35$, approximately), the chances of accepting H_0 and H_1 are equal. The curve on the right (Fig. 3) may be used in the same way for the moderate versus severe classes. There is some overlapping between the two curves, but only at negligible probability levels. Thus the possibility of calling a light infestation severe, or a severe infestation light, is rather remote. Consideration of these two curves will help the reader to understand why gaps were intentionally left between the classes when the infestation limits were defined in an earlier section.

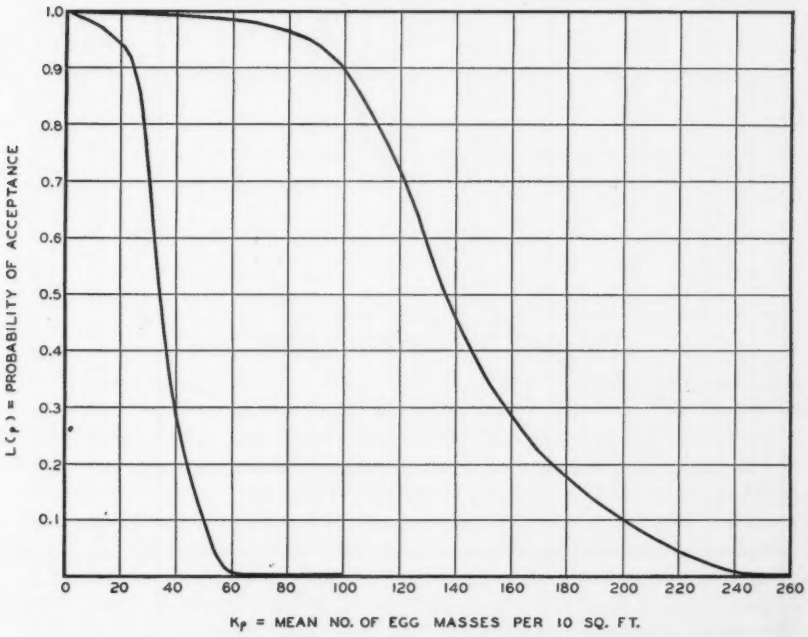

FIG. 3. The operating characteristic curve for light versus moderate infestation classes (left) and for moderate versus severe (right). In both cases, $L(p)$ is the probability of accepting the H_0 hypothesis. These curves apply equally to Sampling Methods I and II.

The operating characteristic curve is calculated from:

$$L(p) = \frac{A^h - 1}{A^h - B^h}, \text{ with } A \text{ and } B \text{ as defined above,}$$

and $$p = \frac{1 - (q_0/q_1)^h}{(p_1 q_0/p_0 q_1)^h - 1},$$

where h is a 'dummy variable' which may be assigned convenient values.

For a given value of h, the value of p, kp, and $L(p)$ may be calculated as shown in Table II. As the accepted probability of error is the same for both sampling methods, the values of $L(p)$ are also the same for both.

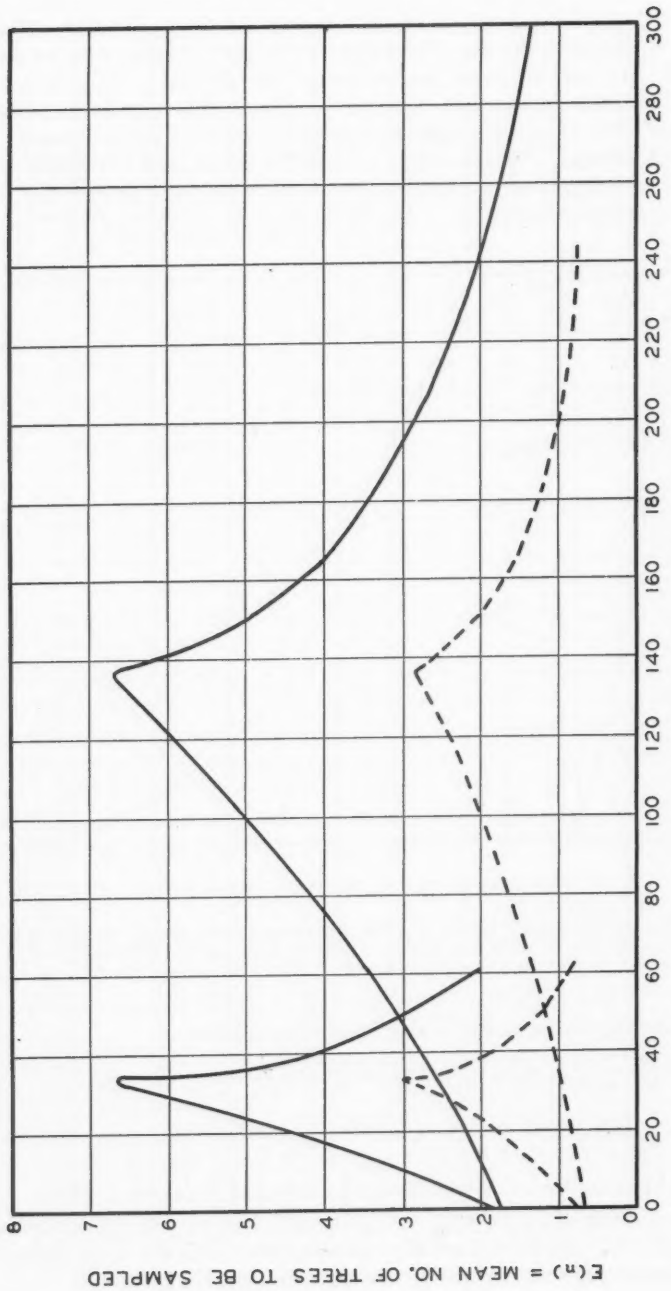

FIG. 4. The average sample number curves for Sampling Methods I (broken lines) and II (solid lines). The curves on the left are for the light versus moderate infestation classes and those on the right for the moderate versus severe.

TABLE II

EXAMPLE OF CALCULATIONS TO ESTABLISH THE OPERATING CHARACTERISTIC CURVES AND THE AVERAGE SAMPLE NUMBER CURVES

(The figures apply to the light versus moderate infestation classes and to Sampling Method I, where $k = 5.232$)

h	p	kp	$L(p)$	$E(n)$
∞	0	0	1.00	0.76
1	4.78	25.0	0.90	2.19
$\frac{1}{2}$	5.62	29.4	0.75	2.55
$\frac{1}{4}$	6.11	32.0	0.63	2.76
$-\frac{1}{4}$	7.26	38.0	0.37	1.79
$-\frac{1}{2}$	7.95	41.6	0.25	1.72
-1	9.55	50.0	0.10	1.27
$-\frac{3}{2}$	11.57	60.6	0.04	0.87
$-\infty$	∞	∞	0.00	0.00

The Average Sample Number Curves

The average sample number curves (Fig. 4) make it possible to foresee the mean number of trees, $E(n)$, which must be sampled by the field parties at any population level. As would be expected, the peaks in the curves occur where populations are borderline between light and moderate or between moderate and severe. At levels of kp which are more definitely in the light, moderate, or severe classes, one or two trees at each sampling point will often suffice when Method I is used. Method II requires, on the average, slightly more than twice as many trees as Method I. It does not require more time, however, because there is less than one-half as much foliage to be examined per tree. It is well to remember that $E(n)$ is the *average* sample number; the indicated maximum of about seven trees (Fig. 4) may have to be considerably exceeded at certain sampling points.

For different values of kp (Table II), $E(n)$ is calculated from:

$$E(n) = \frac{h_1 + (h_0 - h_1)\, L(p)}{kp - s},$$

where h_0, h_1, and s have already been defined for the acceptance and rejection lines.

Application of the Plan

In applying the sequential plan in the field it is convenient to use tabulations (Table III) read from the acceptance and rejection lines rather than the lines themselves. The use of these tabulations is readily demonstrated to field parties.

In August and September, 1953, more than 1000 sampling points were classified in northern New Brunswick with the aid of the sequential plan. This required about 1300 man-days, including all the necessary supervision, car and foot travel, and camp routine. It also provided for a check examination on 30% of the sample branches. A large proportion of the sampling points were located in areas sprayed in 1953, where the infestation class was often intermediate between moderate and severe. This factor has a considerable effect on the expenditure of time (cf. Fig. 4). The number of man-days required per sampling point in other areas will depend largely on the population levels encountered.

TABLE III

SEQUENTIAL TABLE FOR USE BY FIELD PARTIES, READ FROM THE ACCEPTANCE AND REJECTION LINES (FIGS. 1 AND 2)

(Sampling is continued until the cumulative result falls outside the bands into one of the zones)

Tree	Cumulative No. of egg masses per 100 sq. ft.									
	Light vs. moderate band					Moderate vs. severe band				
Sampling Method I										
1	LIGHT ZONE	8	—	59	MODERATE ZONE	42	—	225	SEVERE ZONE	
2		42	—	93		183	—	366		
3		78	—	129		323	—	506		
4		112	—	163		460	—	643		
5		147	—	198		599	—	782		
6		182	—	233		738	—	921		
7		216	—	267		878	—	1061		
8		251	—	302		1016	—	1199		
9		286	—	337		1154	—	1337		
10		320	—	371		1291	—	1474		
Sampling Method II										
1	LIGHT ZONE	0	—	90	MODERATE ZONE	0	—	360	SEVERE ZONE	
2		5	—	126		35	—	498		
3		41	—	162		174	—	637		
4		77	—	198		312	—	775		
5		110	—	231		452	—	915		
6		145	—	266		591	—	1054		
7		179	—	300		728	—	1191		
8		215	—	336		868	—	1331		
9		249	—	370		1005	—	1468		
10		284	—	405		1144	—	1607		
11		318	—	439		1283	—	1746		
12		355	—	476		1420	—	1883		
13		389	—	510		1559	—	2022		
14		422	—	543		1698	—	2161		
15		457	—	578		1837	—	2300		

The greatest advantage of the plan is that no time is wasted in superfluous sampling at points where the infestation falls distinctly into one of the three classes. In severe infestations, where populations over 1000 masses per 100 sq. ft. are not uncommon, one or two trees are usually sufficient. In previous years, with a fixed sample size, it was obvious that time was being wasted under such conditions. The concomitant disadvantage of the plan is the relatively greater amount of sampling required under intermediate conditions. Unless it is particularly important to resolve intermediate populations to the nearest infestation class, an upper limit can be placed on the number of trees to be sampled at any one point. If the cumulative result is still within a band when this number is reached, the point can be classed as 'light to moderate' or 'moderate to severe', and appropriate adjustments made when the infestation map is prepared.

If the foliage is taken to the laboratory for examination, more branches must generally be collected than are needed, especially at remote points that are not easily revisited. For Sampling Method I this is a rather important disadvantage. For Method II, which appears to be greatly preferred by the field parties, it is much less important. Collection time is very low in relation to examination time, particularly when Method II is used.

Acknowledgments

The writer is much indebted to G. B. Oakland, who made helpful suggestions concerning the analysis; to F. E. Webb, who permitted the use of certain field notes in deriving constants for Sampling Method II, and provided the information on the performance of field parties; and to the staff of the Green River Project, who assisted in the fundamental population work.

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STUDIES ON DIPTEROUS PARASITES OF THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (CLEM.) (LEPIDOPTERA: TORTRICIDAE)

IV. *MADREMYIA SAUNDERSII* (WILL.) (DIPTERA: TACHINIDAE)[1]

By H. C. Coppel[2] and M. G. Maw[2]

Abstract

Studies initiated in British Columbia in 1943 showed that *Madremyia saundersii* (Will.), a native parasite with a wide range of lepidopterous hosts in North America, was a parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.). The parasite has been obtained each year since then in moderate numbers and released in infested areas of Eastern Canada. *M. saundersii* deposits macrotype eggs on the integument of host larvae. The first stage larvae penetrate the integument of the host. The larvae attach themselves to tracheal trunks, where they remain throughout the first and second stages, but during the third feeding stage they wander freely within the body, devouring all the contents. The period from egg deposition to adult emergence was 17 to 23 days under laboratory conditions. The life history and habits of the insect are outlined, and are supplemented by general field observations. The immature stages of the parasite are illustrated and described.

Introduction

The tachinid parasite *Madremyia saundersii* (Will.) has been obtained in moderate numbers from collections of the spruce budworm, *Choristoneura fumiferana* (Clem.), made in British Columbia annually since 1943. Wilkes, Coppel, and Mathers (15) included it among the 15 most important parasites of the budworm. Coppel (3) placed its importance at the mid-point of this group with parasitism in certain areas of British Columbia as high as 7.5%; in nearby areas in British Columbia, however, it is almost absent from the parasite complex. Dowden, Buchanan, and Carolin (5) recorded an aggregate parasitism of 14–20% by *M. saundersii* from both larval and pupal collections of the budworm in Colorado, U.S.A. Arrangements were made to rear the parasite from collections from Western Canada and to release them in eastern budworm infestations, where *M. saundersii* has never been abundant. More than 7000 adults have so far been shipped to regions in Ontario, New Brunswick, Newfoundland, and Quebec. The largest numbers were liberated in Ontario and New Brunswick. A small shipment was also sent to New York State, U.S.A.

M. saundersii from British Columbia was reared at the Belleville laboratory on *C. fumiferana*, *Pieris rapae* (L.), and *Pyrausta nubilalis* (Hbn.) to provide material for the descriptive and biological data included in this paper.

Systematic Position, Distribution, and Hosts

In 1889 Williston (16, p. 1922) described a new species of Diptera under the name *Phorocera saundersii*. Aldrich and Webber (1), in 1924, transferred

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the species to the genus *Madremyia* Townsend, the type of which, *M. parva* Tns., they showed to be a synonym of Williston's species. This combination has been used to date. The main distinguishing characters of this genus are the length of the penultimate aristal joint and the presence of an extra row of bristles, three to six in number, outside the usual row of frontals.

M. saundersii appears to be confined to the temperate areas of North America. As a parasite of the spruce budworm in Canada it has been recorded from British Columbia to Newfoundland. As a parasite of other lepidopterous hosts it has been recorded in southern Canada and the northern United States and at higher altitudes as far south as New Mexico and California.

M. saundersii has been recorded only from lepidopterous hosts. Thompson (12) and Aldrich and Webber (1) have published extensive host lists, including species in the families Geometridae, Tortricidae, Noctuidae, Liparidae, and Nymphalidae.

Descriptions of Stages

Adult

Keys for the separation of adults have been published by Aldrich and Webber (1), Coquillett (4), and Townsend (13). Adequate descriptions of the adults have been made by Townsend (14) and Aldrich and Webber (1). Photographs of the adults and drawings of the female have been published by Essig (6) and Hyslop (8) respectively.

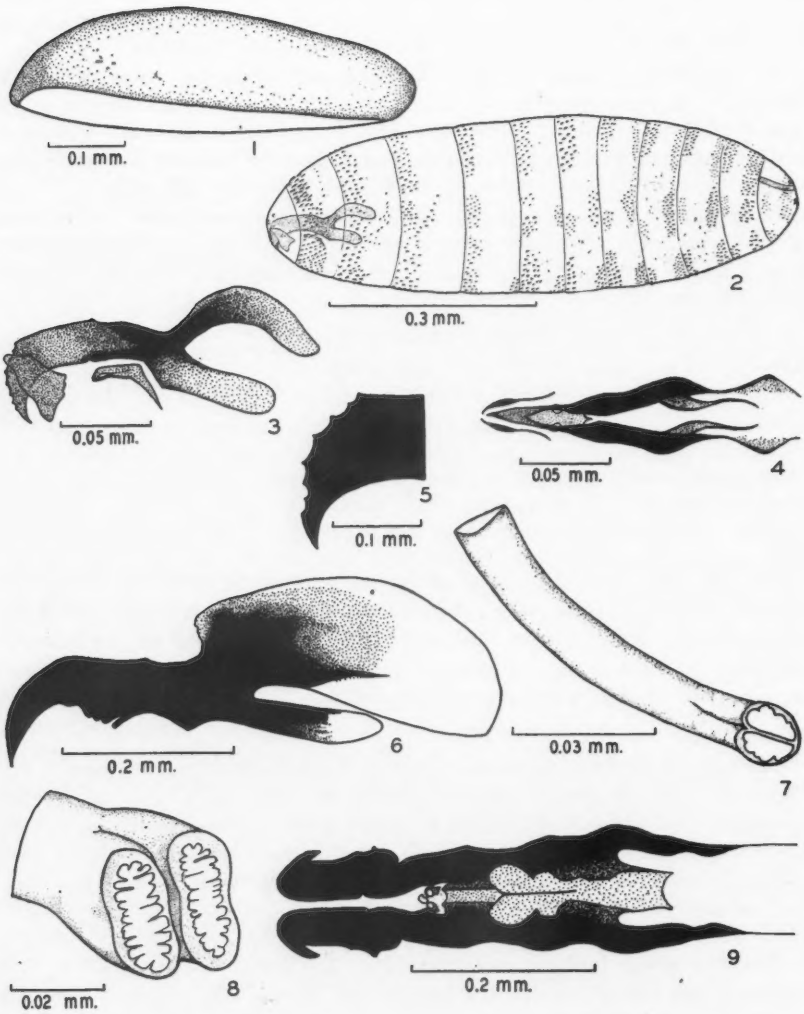
Egg

The egg (Fig. 1) of *M. saundersii* is white; flattened ventrally; broadly rounded at the posterior end; and in lateral view sloping slightly toward the anterior end. It is 0.7 mm. long and 0.25 mm. wide. Its surface is finely etched with faint, irregular hexagonal reticulations. Micropylar openings were not observed at a magnification of 100×.

First Instar

The body of the larva tapers anteriorly and is somewhat truncate posteriorly (Fig. 2). It is of about the same size as the first stage larva of *Phryxe pecosensis* Tns. (9) and ranges from 0.75 to 2.0 mm. in length with an average length of 1.5 mm. The cuticle is colorless and each segment is armed with spines arranged in discontinuous rows. Two conspicuous patches of strong dark spines are found on the 11th segment, one dorsad and the other ventrad of the stigmatal openings. The arrangement of the spines is shown in Table I.

The first instar larva is metapneustic. The two stigmata, on the 11th segment, are slightly above the longitudinal axis. The stigmata resemble closely those found in *P. pecosensis* (9), except that those of *M. saundersii* are less heavily pigmented. Each stigma (Fig. 7) bears two openings with irregular inner margins, the openings being separated by a thin septum. The stigmata are separated by a space equal to the width of each. The felt chambers are lightly pigmented and are approximately four and a half times as long as their diameter. The chambers are directed dorsally from the stigmata at about a 30° angle.



FIGS. 1–9. *Madremyia saundersii* (Will.). 1. Egg, ventrolateral view. 2. First instar larva, showing arrangement of spines, position of posterior spiracles, and the buccopharyngeal armature. 3. Buccopharyngeal armature of first stage larva, lateral view. 4. Buccopharyngeal armature of first stage larva, dorsal view. 5. Tip of first instar mouth hook. 6. Buccopharyngeal armature of second instar mouth hook, lateral view. 7. Posterior spiracle and felt chamber of first instar larva. 8. Posterior spiracle and felt chamber of second instar larva. 9. Buccopharyngeal armature of second instar larva, dorsal view.

TABLE I

APPROXIMATE NUMBERS OF ROWS OF SPINES ON THE DORSAL, LATERAL, AND VENTRAL REGIONS OF *M. saundersii* LARVAE

Stage	Band	Position	Segment										
			I	II	III	IV	V	VI	VII	VIII	IX	X	XI
I	Anterior	Dorsal	4–5 + 1*	4–6	3–4	2–3	3–4	4	2–3	3–4	3	2–4	0
		Lateral	3–4 + 1*	5–6 + 2–3*	4 + 2–3*	4	3–4	3–4	2–3	2–3	2–3	3–4	1–3
		Ventral	6–7	5–6	4–5	3–4	2–4	2	2–3	2	2	2	2–3
	Posterior	Dorsal	0	0	0	0	0	0	1–2	2–3	3–4	4–5	3+
		Lateral	0	0	0	0	3–4	3	3–4	4–5	4–5	3–4	5
		Ventral	0	0	0	2–3	2–3	3–4	3–4	3–4	3–4	3–4	1–4
II	Anterior	Dorsal	6–7	5–7	4–6	3–5	3–4	3–4	2–3	1–3	1–2	1–3	0
		Lateral	3–5	4–6	3–5	4–5	3–5	3–4	3–4	3–4	3–5	4–5	3–4
		Ventral	6+	7–8	6–8	6+	3–5	3–4	3	2–3	3	4	2–4
	Posterior	Dorsal	0	0	0	0	0	0	1	2–3	3–4	6–7	5–6
		Lateral	0	0	1	2–4	4–5	5	5–6	6	6–7	7–8	6
		Ventral	0	0	0	0	6	6–7	6–7	6–7	7–8	6–7	5–6
III	Anterior	Dorsal	3–4	5–7	4	4	4	4–5	2–4	1–3	1	1–2	0
		Lateral	4–5	5–6	4–5	4–5	4–5	2–3	1–2	1	1	2–3	0
		Ventral	4–5	6–7	4–5	3–5	5	3–4	3–4	4–5	3–4	2–3	0
	Posterior	Dorsal	0	0	0	0	0	0	0	0	1–2	7–8	15
		Lateral	0	0	0	0	0	2	2	2–3	3–4	4	17
		Ventral	0	0	0	0	0	0	1–2	1–2	2–3	6	20

* *Row of spines branching from main row.*

The pseudocephalon bears the antennomaxillary complex, made up of a pair of flattened antennae, two pairs of rodlike sensory organs, and several smaller sensory papillae.

The buccopharyngeal apparatus (Figs. 3 and 4) is well developed and unjointed. The two lateral sections converge and the tip bears seven coarse teeth. Lateral plates are found on either side of the hook. The axes of the plates are in an oblique plane, and their anterior parts project dorsoanteriorly. The intermediate portion of the apparatus is moderately long, stout, and moderately pigmented. The salivary plate is large, with a well defined indentation on the anterolateral region. The posterior portion of the apparatus is darkly pigmented in the basal regions and moderately pigmented in the remaining portions of both the dorsal and ventral wings. The dorsal wings are highly arched whereas the ventral wings are straight throughout their length. Both the dorsal and the ventral wings converge slightly posteriorly.

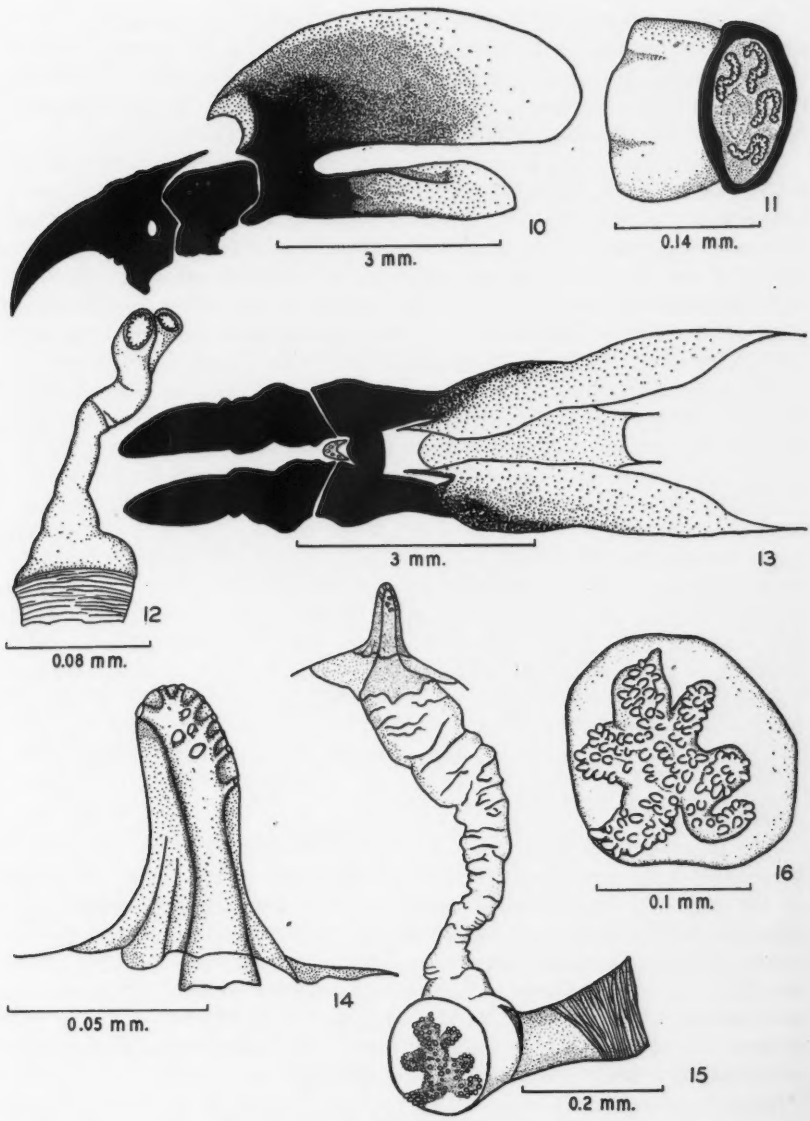
Second Instar

The second instar larva ranges in length from 2.0 mm. to 5.6 mm. with an average length of 4.2 mm. The cuticle is colorless as in the first stage and each segment is armed with spines of nearly uniform size and structure and of moderate strength. The rows of spines run more or less continuously around the larvae on the first three and the last four segments. On segments IV to VII, the rows of spines are broken both dorsad and ventrad of the lateral rows. This gives the appearance of lateral patches on these segments. The patches of dark spines dorsad and ventrad of the stigmata resemble those of the first instar. The approximate number of rows of spines per segment is shown in Table I.

As far as could be determined, the second instar is metapneustic. The longitudinal tracheal systems end in a blind pouch just under the cuticle, laterally, at the posterior margin of the first thoracic segment. The two posterior spiracular plates (Fig. 8) are light brown and each one has two spiracular openings, each with an irregular border. The felt chambers are comparatively short and are about twice as long as broad.

The antennomaxillary complex is similar to that of the first stage except that the two sensory rods are surrounded by a raised, sclerotized ring. No small sensory organs were observed.

The buccopharyngeal apparatus (Figs. 6 and 9) is well developed and unjointed. The paired anterior hooks turn abruptly downward. In lateral view, the intermediate portion of the apparatus is nearly straight along the dorsal margin except for a small dorsal protuberance. The ventral margin of the intermediate section has two protuberances, the anterior one rough in outline and the posterior one smooth in outline. The posterior section of the apparatus is made up of the large, bladelike dorsal wing, ending in a semi-transparent tail-piece, and a small ventral wing. In dorsal view the apparatus appears relatively stout throughout its length. The paired sections are united in the intermediate region and the ventral wings unite to form a pharyngeal trough.



FIGS. 10–16. *Madremyia saundersii* (Will.). 10. Buccopharyngeal armature of third instar larva, lateral view. 11. Posterior spiracle and felt chamber of third instar larva. 12. Anterior spiracle and felt chamber of third instar larva. 13. Buccopharyngeal armature of third instar larva, dorsal view. 14. Tip of prothoracic cornicle. 15. Pupal respiratory apparatus. 16. Internal spiracle.

Third Instar

The average length of third instar larvae is 7.0 mm., with a range of 5.6 mm. to 9.5 mm. The larvae are robust, and darker than in the preceding stages.

The cuticular spines are broad, flat, and, except for the rows on the first two and the last segments, difficult to observe because of the absence of pigments. The distribution of the spines is shown in Table I.

The third instar larva is amphipneustic. The anterior spiracles (Fig. 12) project from the posterior border of the first body segment. They are of simple form, being nothing more than a single tapering tube terminated by a pair of orifices. The posterior spiracles (Fig. 11) are in a shallow depression dorsad of the transverse axis of the larva, on the 11th segment. They are dark around their circumferences and lighter toward their centers. Each plate contains four serpentine slits. The felt chambers are short, about as long as broad, and of large diameter.

The antennomaxillary complex is similar to that of the second instar except that the components are much larger. The antennae are raised above the surrounding surfaces and appear to be made up of two distinct segments.

The buccopharyngeal apparatus (Figs. 10 and 13) is well developed, with three distinct sections: anterior, intermediate, and posterior. The points of separation are distinct. The anterior section is comprised of a pair of stout hooks, each with a dorsal and a ventral horn pointing posteriorly. Laterally, each hook has a large foramen near its posterior border. The intermediate section is stout and roughly H-shaped in dorsal view. Anterior to the crosspiece of the H is the U-shaped salivary plate. The posterior section is made up of two large dorsal wings, which are heavily pigmented at their bases but lightly pigmented in their posterior, bladelike sections. A small thick hook projects anteriorly from each wing. Laterally the ventral trough appears as a small wing with nearly parallel borders and a heavily pigmented base.

Puparium

The puparium has been illustrated by Greene (7) and Ross (10) and the external features have been described by Greene (7, p. 16). The central area of the stigmatal plates is much lighter in color than the surrounding edges. The anterior spiracles appear as small, light brown papillae near the posterior margin of the prothoracic segment. The prothoracic spiracles (Fig. 15) are found on the lateral surfaces of the fourth segment as small but easily seen projections. The cornicle (Fig. 14) has at least 12 respiratory orifices. Each internal spiracle (Fig. 16) has approximately 125 respiratory papillae arranged on radiating branches at the end of the atrium.

Reproductive Systems

The reproductive system of the male is similar to that of *P. pecosensis* (9) except that the accessory glands lie closer to the vasa deferentia in *M. saundersii* and the ejaculatory pump is more nearly oval in shape. A brief description of the system is given by Townsend (14).

The female reproductive system is very similar to that of *P. pecosensis* (9) except that in *M. saundersii* the ovaries have about 10 ovarioles, each of which produces about nine eggs. The accessory glands of *M. saundersii* are only about half as long as those found in *P. pecosensis*.

Life History and Habits

Methods

Parasites reared from the spruce budworm collected in British Columbia were handled as described by Arthur and Coppel (2). The adults were fed crushed raisins and a 10% aqueous solution of honey. The cages were sprayed twice daily with tap water.

Data on preoviposition and oviposition were obtained by placing budworm larvae in cages containing mated females. When budworm larvae were not available, the larvae of *Pieris rapae* (L.) and *Pyrausta nubilalis* (Hbn.) were used.

All rearing was carried out at 23° C. and 60% relative humidity.

Life History

Mating occurs readily under laboratory conditions when the female is newly emerged (one day old) and the males two or three days old. The pairs remain in copula from 20 min. to two hours.

The preoviposition period varied from five to seven days. Soon after an egg is deposited, the young larva cuts an opening through both the chorion of the egg and the integument of the host. From two to three days were spent in the first instar, three to four days in the second, and two to three days in the third; female larvae required a longer period for development, usually one day longer. The puparium was usually completed within 24 hr. after the third instar larva left its host. Nine to 12 days after the puparium was formed, the adult emerged; the female required the longer period (for 50 of each sex, an average of 9.8 days for males and 10.6 days for females). Adult females lived 20 to 60 days and males to a maximum of 25 days.

Habits

Laboratory Observations

After the preoviposition period, the female lays small numbers of eggs each day. She approaches the host and appears to examine it for a few seconds. Oviposition takes place quickly as the female rests momentarily on the back of the host. Several eggs may be deposited on a single host, the dorsal and lateral regions of the thorax receiving the greater number. During her life, a female usually deposits 75 to 100 eggs. Some difficulty was encountered by the adults in depositing eggs on setose host larvae. Usually, only one parasite emerges from each host, although as many as five puparia were obtained from substitute hosts used in the laboratory.

The parasite emerges from the ventral surface of the chorion at the end of the egg and immediately enters its host. It then attaches its posterior end to a branch of the trachea and remains in the fatty tissue surrounding the

alimentary canal. It feeds and remains attached to the host's tracheal system until it reaches the third instar. The attachment to the trachea is then broken and the larva feeds voraciously upon the host until it is mature. The larva cuts a hole in the cuticle of the host, crawls out, falls to the ground, and pupates in the soil. The parasite, in the mature larval instar, emerges from either the larva or the pupa of the host.

It is not definitely known in what instar the parasite overwinters. However, it probably remains as a larva in diapause (first or second instar) in one of its many hosts. When *P. nubilalis* was used as a host for rearing *M. saundersii* the development and subsequent emergence of the mature parasite larva was often delayed as long as 38 days. This delay may have been influenced by the host larva normally entering diapause in this stage. Attempts to overwinter the adults in the laboratory were unsuccessful.

Field Observations

Adults of *M. saundersii* emerged from the budworm in British Columbia early in July. They have been obtained from an elevation of 1000 ft. during the first week in July, from 2000 ft. from July 7 to July 21, and from 3000 ft. from July 21 to August 7. Specimens were collected in very small numbers at the lower elevations (below 1000 ft.) and in the largest numbers from the central point of budworm infestation (2000 to 4000 ft. elevation). Two puparia were sometimes reared from one field-parasitized budworm but one is the usual number.

Since *M. saundersii* emerges from the budworm relatively early in the season, at least two generations may be expected each year. One complete generation develops at the expense of the budworm. A second generation develops later in the summer on a host in which the parasite could overwinter as an immature larvae. Although no precise information exists there is the possibility of three generations per year in certain areas (11).

Preliminary studies on the effects of multiparasitism on the parasite complex indicated that budworm larvae already parasitized by *Phytodietus fumiferanae* Rohw. are sometimes parasitized by *M. saundersii*. In all instances, *M. saundersii* completed its feeding stage very rapidly and left insufficient food for *P. fumiferanae* to complete its development. The puparia of *M. saundersii* are often destroyed by the hyperparasite *Amblymerus verditer* (Nort.).

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THE IDENTIFICATION OF ADULT FEMALE *AEDES* MOSQUITOES (DIPTERA, CULICIDAE) OF THE BLACK-LEGGED GROUP TAKEN IN THE FIELD AT CHURCHILL, MANITOBA[1]

By W. E. Beckel[2]

Abstract

The present status of the taxonomy of the black-legged species complex within the genus *Aedes* is discussed. The complex in the Churchill region includes *Aedes nigripes* (Zetterstedt), *A. impiger* Dyar (equals *A. nearcticus* Dyar), *A. pionips* Dyar, *A. communis* (De Geer), *A. punctor* (Kirby), *A. hexodontus* Dyar, *A. cinereus* Meigen, and may involve *A. intrudens* Dyar, *A. implicatus* Vockeroth (equals *A. impiger* Dyar), and *A. sticticus* (Meigen). The difficulty of separation of the females with the existing taxonomic characters is pointed out, especially if badly rubbed specimens or specimens preserved in alcohol are to be studied. Characters are then presented to separate all the species in the complex except *A. punctor* from *A. hexodontus* and *A. intrudens* from *A. communis*. Since, in the Churchill region, the larvae of *A. punctor* are rarely found, and those of *A. intrudens* have not yet been found, these exceptions are of minor importance.

Introduction

The *Aedes* black-legged complex poses many problems in taxonomy. In the Churchill, Manitoba, region the complex consists of *Aedes nigripes* (Zetterstedt), *A. impiger* Dyar (equals *A. nearcticus* Dyar (3)), *A. pionips* Dyar, *A. communis* (De Geer), *A. punctor* (Kirby), *A. hexodontus* Dyar, *A. cinereus* Meigen, and may involve *A. intrudens* Dyar, *A. implicatus* Vockeroth (equals *A. impiger* Dyar (3)), and *A. sticticus* (Meigen). The larvae of all the species except the last three have been definitely found in Churchill, and those of *A. implicatus* are probable. It has always been considered possible to identify adult specimens of any species if associated larval skins were available. But in the Churchill region I have observed variation in such larval characters as the number of comb scales, the number of prothoracic hairs, and the position of the tuft of hairs on the anal tube in relation to the last tooth of the pecten. These variations cast some doubt on positive identification even when the larval skin is associated with the adult. In most cases, however, it is not possible to examine the larvae of the species of mosquito to be identified. The males of most species can be separated by characters of the genitalia; but it is the female which is of major interest.

In the past the color of the scales on the mesonotum has been used to separate adult females. In most species I do not find this character alone of sufficient value for separation. If one compares a relatively small number of specimens, taken from one area at a time, particularly if they are reared from larvae living in fairly constant conditions, the color pattern of the scales appears constant enough to warrant its use. But if females reared in their

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natural pools are to be studied throughout the season, then the color pattern of the scales is only of value if the observer has become acquainted adequately with the range of color patterns which occur in the populations at any one time and in the change of color of the scales with age. Females of *A. hexodontus* have been collected in large numbers for physiological research in the Churchill laboratory and whereas specimens with dark brown sides of the mesonotum and a golden central stripe were noted at the beginning of the season, specimens with a change in color to light golden sides with a brown central stripe were noted close to the end of the season. Also a color change from a dark bronzy brown to a very light gold has been observed in the mesonotum of *A. nigripes* as the season progressed.

These variations within one geographical location add to the difficulty of separation of the species. *A. nigripes* is normally considered separable from *A. hexodontus* since it is more hairy, has excessive white scaling at the base of costa and radius of the wing, and has more setae on the post pronotum than *A. hexodontus*. However in the Churchill region I have seen specimens, identified from larval skins as *A. nigripes*, which could not be separated from *A. hexodontus* even by a combination of all three of these characters.

A. impiger can be readily separated from *A. nigripes* and the rest of the complex by the character of its tarsal claw (3) but even this character is not useful for separating *A. impiger* from *A. implicatus*.

A. communis reared in the laboratory from the Churchill region shows a fairly constant, distinctive mesonotal color pattern. However, very few specimens are collected in the field since *A. communis* appears to be nonbiting in this region. It is only collected in general sweeps under which conditions it is denuded of scales. The color pattern is very close to that of *A. intrudens* and *A. implicatus* and misidentifications of these species may have been responsible for records of biting of *A. communis* elsewhere.

A. pionips is easily separable from others in the complex if its mesonotal scales are intact since its mesonotal pattern is fairly distinct. Only when badly rubbed does this species become a problem.

A. cinereus is separable on the basis of its smallness and the reduction of white scales on the dorsum of the abdomen and a brown patch of scales on the procoxa. In badly rubbed specimens, however, these characters are of no value.

A. hexodontus is by far the most common species in the Churchill region and has a most variable mesonotal pattern, as mentioned. No good characters of use for its separation from all *A. punctor* in this region have been discovered. As described by Knight (2) the type variety of *A. punctor* has the base of costa dark scaled or rarely with a few pale scales. This is true of the few specimens of *A. punctor* from the Churchill region. In *A. hexodontus* a considerable patch of pale scales is present. The tundra variety of *A. punctor* cannot be separated from *A. hexodontus*. However, based on the numbers of larvae found, very few *A. punctor* occur in the Churchill region.

Observations

The above comments indicate that mesonotal color pattern is unreliable for separation of most of the black-legged complex. If population studies are to be made and net-collected specimens are to be used, characters must be found to separate badly denuded specimens and even those preserved in alcohol. One such character recently used to great advantage by Vockeroth (3) is the post procoxal scale patch. *A. pionips*, *A. hexodontus*, *A. punctor*, *A. nigripes*, *A. impiger*, and *A. implicatus* have this scale patch; in *A. communis*, *A. cinereus*, *A. intrudens*, and *A. sticticus* this area is bare. I have discovered other characters while studying large numbers of adult female mosquitoes used in our laboratory research at Churchill. They apply to rubbed specimens and to those preserved in alcohol.

Scaling of the Probasisternum

In *A. communis*, *A. nigripes*, *A. impiger*, *A. intrudens*, *A. implicatus*, *A. cinereus*, and *A. sticticus* the probasisternum (Fig. 1, *PBS*), in particular the most posterior part, is bare. Occasionally, in the specimens observed, a stray scale or two is found opposite the proepisternum on the basisternum. In *A. hexodontus* and *A. pionips* the probasisternum has white scales. In *A. punctor* scales have been found on the majority of specimens observed but not on all. Of the specimens observed in the Canadian National Collection the results were as follows: Brockenhurst Hants, England, one specimen, basisternum scaled; Epping Forest, Essex, England, two specimens, basisterna scaled; St. Anthony, Nfld., one specimen, basisternum bare; Waskesiu, Sask., three specimens, basisternum scaled in two, bare in one; Moose Factory, Ont., basisternum scaled in five specimens, bare in two; and in the Churchill, Man., collection three specimens were available, all had scaled basisterna.

The scaling on the probasisternum of the *A. punctor* observed was reduced in comparison with that of *A. hexodontus*. When scales were present there were only a very few on *A. punctor*. But a large series of females from three or four widely separated regions would be necessary to clarify the position of *A. punctor*. In most of the specimens of *A. pionips* and *A. hexodontus* observed there was a considerable number of scales present.

Abbreviations of Labels of Figures

AAE.....anterior anepisternum
ALM.....anterolateral mesonotum
APN.....anterior pronotum
ASC.....antescutellar space
AST 1.....abdominal sternite 1
CS.....cervical sclerite
KES.....katepisternum
L.....light reflecting line
ME.....meron
MEP.....mesepimeron
MS.....mesosternum
MTS.....metasternum
NM.....neck membrane
OC.....occiput
PBS.....probasisternum
PES.....proepisternum
PLM.....posterolateral mesonotum
PMM.....post metasternal membrane
PPN.....posterior pronotum
SC.....scutellum
SPB.....sternopleural bridge
VC 1.....first ventral condyle
VC 2.....second ventral condyle

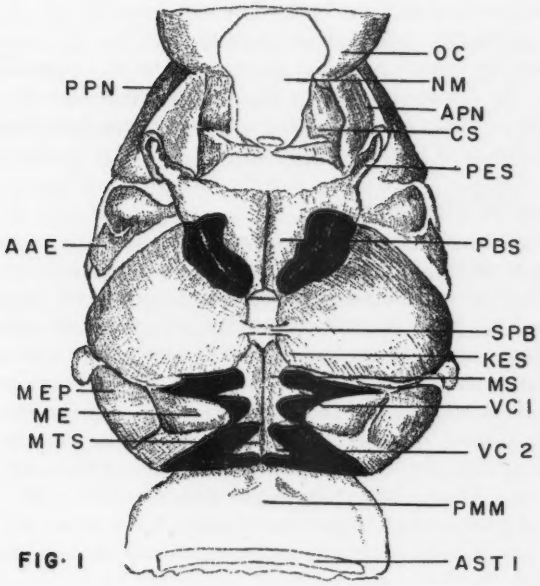

FIG. 1

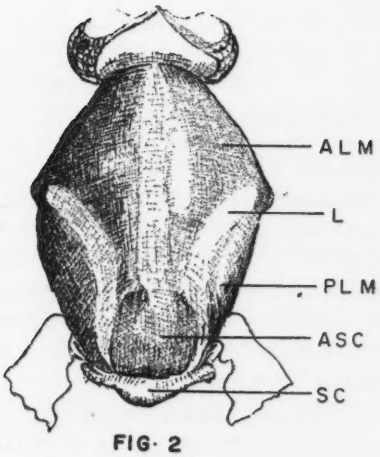

FIG. 2

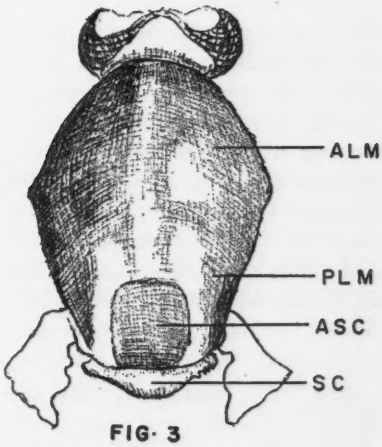

FIG. 3

FIG. 1. A ventral view of the thorax of *Aedes hexodontus*.
FIG. 2. A dorsal view of the mesonotum of *Aedes hexodontus*.
FIG. 3. A dorsal view of the mesonotum of *Aedes nigripes*.

NOTE: Abbreviations are explained on p. 326.

The probasisternum is seldom denuded of scales in net-collected specimens owing to the protection afforded the basisternum by its anterior ventral position between the procoxae. But the specimens of *A. punctor* with bare basisterna may have lost their scales through rubbing since only a few are present originally. These would then key to *A. implicatus* but can be separated from it by differences of the tarsal claws.

Color of the Denuded Mesonotum

If the denuded mesonotum of *A. hexodontus* is held with the anterior end away from the observer, in a bright light under a binocular microscope, two lines, casting light gray reflections in contrast to the black mesonotum, are observed extending anterolaterally from the anterolateral margins of the antescutellar space to about the mid-lateral border of the mesonotum (Fig. 2, *L*). Similar lines are noted in *A. punctor*, *A. implicatus*, *A. pionips*, *A. communis*, *A. intrudens*, and *A. sticticus*. In *A. nigripes* and *A. impiger* these lines are absent; the anterolateral points of the antescutellar space merely extend straight forward for a short distance. Often the mesonotum has a brown cast. In *A. cinereus*, a species which occurs in small numbers in the Churchill region, the denuded mesonotum lacks any lines as seen in *A. hexodontus* and is a lighter brown in contrast to the black or dark brown of *A. nigripes* or *A. impiger*.

Mesonotal Setae

In the Churchill region the number of setae in the anterolateral section of the mesonotum and the posterolateral section (Figs. 2 and 3, *ALM*, *PLM*) has been found to separate *A. hexodontus* from *A. pionips*. In badly rubbed specimens, using only the post procoxal scale patch and the scales of the probasisternum, the species are inseparable. However, in *A. pionips* the average number of anterolateral setal follicles has been found to be 23 (S. D. $\pm$ 3.5); in *A. hexodontus* the average number is 45.9 (S. D. $\pm$ 7.5). The average number of posterolateral setal follicles in *A. pionips* is 42.8 (S. D. $\pm$ 6.6); in *A. hexodontus* it is 86.6 (S. D. $\pm$ 14.0). In less than two and one half per cent of the population will there be overlap. Counts made on *A. hexodontus* from Padlei, N.W.T., and the Alaska highway show numbers similar to those found at Churchill. For *A. punctor*, on the basis of the few specimens observed, the numbers are similar to those for *A. hexodontus*.

The small form of *A. communis* in the Churchill region, mentioned by Hocking (1), has an average number of anterior lateral setae of 16.4 (S. D. $\pm$ 0.5); of posterolateral setae 31.6 (S. D. $\pm$ 0.5). This is a good character for separating it from *A. hexodontus*. The large form of *A. communis*, indistinct in the Churchill region but seen at least in the Padlei district, has numbers of setae which overlap with the numbers for *A. hexodontus*. The difference in numbers of setae in small and large forms of *A. communis* is further evidence of two entities within the species.

Scales on the Post Metasternal Membrane

The post metasternal membrane (Fig. 1 *PMM*) is also of interest taxonomically. This membrane extends from the sclerotized region around the metafurcal pits to the first abdominal sternite. In *A. pionips* there is a patch of white scales on this membrane on each side of the mid-line, separate from and anterior to the scales of the first abdominal sternite. Usually there are 15 or more scales. This area is bare in most specimens of *A. hexodontus* and *A. punctor*; but there may be from one to as many as 12 scales. Further work on the characteristics of this scale patch is needed and should be done on alcohol preserved specimens or on recently killed specimens since on dried ones it is very difficult to see.

Using all the characters outlined above it is possible to separate most of the species of the black-legged complex in the Churchill region. It is still difficult to separate *A. hexodontus* from some varieties of *A. punctor* and to separate *A. communis* from *A. intrudens*. At present Vockeroth (3) separates these latter two only on the color of the mesonotal scales. The larvae, however, are quite distinctive and to date no *A. intrudens* larvae have been found in the Churchill area. One observation has been made, however, of an *Aedes* which keys to *A. communis* landing on the clothes and showing an interest in feeding. It is possible that this was *A. intrudens* or some yet unrecorded species. As mentioned *A. punctor* larvae are found only rarely.

Key to the *Aedes* Black-legged Complex in the Churchill, Manitoba, Region

1. Color pattern of denuded mesonotum showing light gray lines extending anterolaterally from the antescutellar space, the rest of the mesonotum black with grayish reflections (Fig. 2)..... 2

   Color pattern of denuded mesonotum showing no gray lines (Fig. 3); scutellum has grayish reflections; mesonotum uniform black or has two bluish black central stripes and the anterolateral portion brownish, or is all light brown..... 6

2. Posterior portion of the probasisternum with white scales; post procoxal scale patch present..... 3

   Posterior portion of the probasisternum bare..... 4

3. Post metasternal membrane with 15 or more scales, posterior portion of the third, fourth, fifth, and sixth abdominal sternites with brown scales ventrally; setal follicles on anterolateral mesonotum 23 (S. D. ± 3.5); on posterolateral mesonotum 42.8 (S. D. ± 6.6); small patch of yellowish white scales at base of costa and radius.....*A. pionips*

   Post metasternal membrane bare or with two or three scales, rarely with as many as 12; posterior portions of the third, fourth, fifth, and sixth abdominal sternites with white scales, rarely with a few brown scales ventrally; setal follicles on anterolateral mesonotum 45.9 (S. D. ± 7.5), on posterolateral mesonotum 86.6 (S. D. ± 14.0); extensive patch of grayish white scales at base of costa and a few at base of radius.....*A. hexodontus*

   Post metasternal membrane as in *A. hexodontus*; scales on the probasisternum reduced to a few; many brown scales on the posterior portions of the abdominal segments; no white scales at the base of costa or radius or rarely one or two on costa.....*A. punctor*

4. Post procoxal scale patch present; tarsal claw resembling that of *A. impiger*..*A. implicatus*

   If posterior portion of probasisternum rubbed bare of scales and tarsal claw resembles that of *A. nigripes*.....*A. punctor*

5. Lower mesepimeral bristle follicles absent.....*A. sticticus*

   Lower mesepimeral bristle follicles present.....*A. communis*
   A. intrudens

6. Probasisternum bare, post procoxal scale patch absent, mesepimeral bristle follicles absent.....*A. cinereus*

   Probasisternum bare, post procoxal scale patch present, mesepimeral bristle follicles present..... 7

7. Tarsal claw with spur short, not extending half way down the shaft and not parallel to it.....*A. nigripes*

   Tarsal claw with spur long and extending over half way down the shaft and almost parallel to it.....*A. impiger*

Acknowledgments

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